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A SPECIAL ISSUE TO MARK

THE EIGHTIETH BIRTHDAY OF R. E. HOLTTUM, 1975

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RICHARD ERIC HOLTTUM, 1975
at the Herbarium, Botanic Garden, Singapore
photograph by Ismail bin Ahmad

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Dr. R. E. HOLTTUM: An Appreciation

by

B. MOLESWORTH ALLEN

Los Barrios, Spain

Dr. Holttum when writing about the classification of the Leptosporangiate ferns, most of which in the past were united in the Polypodiaceae, stated that "these 'modern' ferns are so extremely varied in form and in the details of all their parts, that no one man could pretend to a critical knowledge of them all, even as to their assignation to genera."

It is strange that he should write this, for his amazing faculty for critical taxonomic interpretation has enabled him to understand so much about these living ferns, both in the field and herbaria. Thus he may well have come as near to having just this critical knowledge about which he writes, as any one man may possibly ever have. Future pteridologists will have not only the advantage of our present-day work, but computers will be used to store much of the knowledge that people of Dr Holttum's age have had to keep in their heads. So although there will possibly be a more complete taxonomic and cytological understanding of the world's ferns in the future, this will surely be a combination of man and his aids, and not held by one man alone owing to the limit of our brain power.

The steps that Holttum stands on today were made firm by Carl Christensen who brought fern classification into the 20th century, and by the important morphological work of Bower and others. In turn each pteridologist was fortunate in having the published works of great thinkers of the past who were responsible for these higher steps from which Christensen and Copeland worked.

No doubt Holttum was fortunate in that fate pointed the way at the beginning of his career, which started as a palaeobotanist under the guidance of no less a scientist than Dr Seward. This gave him an excellent background for the phylogeny of the living ferns when he arrived in Singapore and commenced his taxonomic work, which he was to continue for the next 40-50 years. Again, the area was a fortunate choice; its rich fern flora with so many distinct and unrelated genera must have given him much scope for his enquiring mind. The many relic ferns growing in their natural environment, gave living examples of evolutionary evidence towards a new understanding of the ancestry of different genera and their relationship. The hot, wet climate of Singapore and the Malay Peninsula, without such natural calamities as typhoons and long droughts, was conducive to the continuation of these primitive types of ferns, many of which were not greatly changed from their ancestors. *Matonia* is one such example of a family once widespread in Mezozoic times and some fossils have been found with almost unchanged frond shape. The distribution of *Matonia pectinata* is now extremely limited and is confined to a relatively few hill and mountain ridges in the Malay Peninsula and Borneo, growing where the soil is leached and poor, and where it is less likely to suffer competition from the surrounding lush tropical plantlife.

All this was at his doorstep so to speak, and he made the most of it which many of us have not done, and no doubt he was helped and guided by Copeland's work on Philippine ferns. One assumes that during these years his fertile mind was gathering and storing information on the classification and evolution of the vast array of the ferns before him. He also assimilated much knowledge of the flowering plants as well.

Then in Singapore between 1942-46 he was able to correlate this knowledge, for being cut off from the outside world he was able to work in the herbarium of the Singapore Botanic Gardens, almost without interruption. This resulted in the impressive taxonomic publication on the ferns of the Malay Peninsula and Singapore. In the course of this work, significant facts came to light which altered much of the previously accepted concept of the fern classification of Christensen and others. He also pointed out that there were, at least, several families which needed far more study especially in field observation, one of these being the Thelypteridaceae. He kept *Thelypteris* more or less together thus apposing Copeland (Genera Filicum 1947) who contended that this generic name was invalid, *Lastrea* being the legimate one. Whilst not actually disagreeing with this, Holttum maintained that many changes would have to be made in this group of ferns, and until this was done, *Thelypteris* should stand. As we know, it is a revision of this vast and complex family that Holttum himself has undertaken, and from his active brain we are seeing these ferns in a new light, and currently a series of new combinations and genera are emerging. He has also proposed the conservation of the name *Thelypteris.*

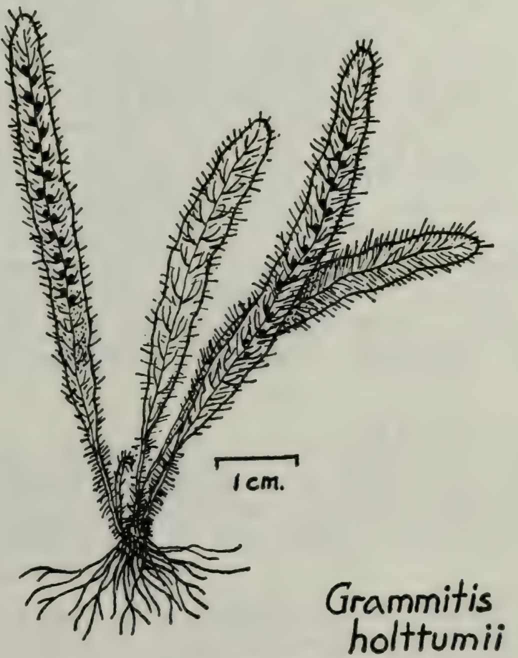
So the publication of the Ferns of Malaya in 1954 with its appendix containing cytological notes of a 100 Malaysian ferns by Professor Manton, began a new era towards the knowledge and understanding of these tropical ferns. At last there was a critical study of this area with up to date name combinations basinyms and sufficient synonyms from which one could work.

As those of us who had followed Christensen, Bower and Copeland (and for me, Dr Holloway) in our formative years, this book as well as his papers on classification, meant yet another pteridological step upwards. Living in Malaya at the time, this publication began a new era for me also. I arrived with a copy of Beddome's "Ferns of British India, Ceylon and the Malay Peninsula" (1892), and a separate of Holttum's "The Common Ferns of Singapore" which had been written for the Singapore Naturalist in 1924. (It was almost impossible to obtain copies of van Alderwerelt van Rosenburgh's handbook on the ferns of the Malayan Islands).

The diversity of the ferns with so many unfamiliar genera, not to mention the richness of the species of these tropical rain forests, was enough to daunt anyone without constant access to herbaria and a botanical library. Ridley's "Ferns of the Malay Peninsula" (1926) was very limited in its list of species, whilst many of the names used were difficult to trace, so that it helped only in a small way. I found that Holttum's key in his paper together with the notes on the ferns, gave a good introduction to the genera one encountered every day, but the vast number of other ferns one saw in the jungle was over-powering. It was a lengthy business, often empirical. to try to determine species, usually ending in a deep depression of doubt which hardly encouraged intelligent collecting, unless one was a collector by instinct So Ferns of Malaya made an enormous difference to those interested in the S. E. Asian ferns.

My association with Dr. Holttum, who was a friend of my husband's parents, has spanned many years, but it differs from most fern botanists in as much as I was never long enough in any botanical department to undertake fern research, so reluctantly became a field botanist, observing and collecting. Holttum never failed to give me encouragement in this, especially when it became tedious. It was stimulating to be in the jungle with him, for his field knowledge, not only of ferns, but also of the angiosperms, was immense, as was his enthusiasm. An interesting plant would be heralded by "a-ha, a-ha", as he bent to look at it and use his lens. On these periodic field trips I learned about tropical botany; he pointed out the strange stamens of Lauraceae, and the amount of caulifery in these rain forests. He seemed untroubled by the continual heat and high humidity, and the rough jungle floor affected him far less than me, even although he had suffered an attack of polio after the war. He was an easy houseguest having continual good spirits, and only once do I remember that these deserted him. It was when he brought the sad news of the death of our mutual friend, A.H.G. Alston in 1958. The passing of this gentle person cast a shadow over our trip that time, which was to see the extent of *Cyathea polypoda* on Mt. Kledang near Ipoh, where it had been locally common.

Holttum encouraged selective collecting, stressing the importance of ecological factors, and although not, I think, a patient man especially with what he considered stupidity, he would give painstaking help to the student of any branch of botany. He also had the gift of being able to impact his knowledge easily, which is reflected in many of his students during his professorship at the University of Malaya in Singapore, who have since become competant botanists. He wrote in simple language to encourage the beginner and his "Plant Life in Malaya" (1954) is an excellent example of simplicity and erudition.



The output of work is staggering when one realises that apart from the Ferns of Malaya he published a companion volume on the orchids; a horticultural textbook "Gardening in the Lowlands of Malaya" (1953) as well as the monographs on gingers and bamboos and the current one on the Thelypteridaceae. Any one of these could be considered the culmination of a life study.

Mention must be made of the enormous help given to the field botanist by publications of the vegetation of specialised localities. The Ferns of Mt. Kinabalu (1934) by Christensen and Holttum in which many species were described, is one of these. I speak from experience, having climbed this exciting mountain, for the abundant fern flora, although having close affinities with the Malay Peninsula, has interesting endemics and a temperate element from the southern hemisphere. So much of this could be appreciated by having read this publication first. Although much more is now known of the ferns there, this paper remains important, not only in the enumeration of the species, but also for its field notes.

Dr. Holttum's energy seems unabated and he still travels widely, not only in the pursuit of ferns and to receive well deserved honours, but to visit his daughter and grandchildren in Australia, which he and his wife have just done. So we wish them well with many happy years ahead.

Richard Eric Holttum, *Croix de Guerre*

A Note

by

H. M. BURKILL

Royal Botanic Gardens, Kew

Holttum's autobiographical note in *Flora Malesiana Bulletin* 28 (1975): 2477-500 contains an omission, in part at least self-effacing, but I am sure its honourable nature is of sufficient interest to bring it to the attention of his friends and colleagues. He refers very briefly to his service in the Friends' Ambulance Unit during the Great War of 1914-18. He went up to St. John's College, Cambridge, in October 1914 and took Class I Honours in the Natural Sciences Tripos, part 1, in June, 1916. A normal university curriculum would lead on immediately to the completion of the degree course in the following year. But conditions were not normal and instead he broke the university timetable to join the Friends' Ambulance Unit for service in France, his university career being completed only after peace had been restored. His service records, preserved in the Library of the Religious Society of Friends in London run: date of joining 12/7/1916; training at Jordans 12/7-1/8/1916; ward orderly, St. George's Hospital, London, 3/8-16/12/1916; in France: posted to Headquarters Instructional School 2/7/1917; cook Section Sanitaire Anglaise 19 27/1/1917; steward, S.S.A. 19 25/9/1918; left unit 7/1/1919. This service with the French Army was recognised by the French Government by decoration with *La Croix de Guerre*, the citation for which reads:

> ECKERSLEY, STANLEY. B.; HEALD, ALFRED; HOLTTUM, R. ERIC; JONES, JAMES; WILSON, ANTHONY L.; WILMOT, HERBERT R.; WRIGHT, HERBERT
>
> Ordre du Régiment 20 Janvier 1919
> 'Convoyeurs à la Section Sanitaire Anglaise 19, ont fait preuve en toutes circonstances sous le feu de l'ennemi de courage et de dévouement aux blessés aux cours des opérations auxquelles cette section a pris part. (Flandres, 1917; Somme — Mars-Avril, 1918; Marne — Mai, Juin et Juillet, 1918; Champagne — Octobre, Novembre, 1918.)'

[as in H. Wright: *Two Years with the French Army: Section Sanitaire Anglaise 19*, Pelican Press, London, 1919, p. 117. Also in Meaburn Tatham & James E. Miles (Editors): *The Friends' Ambulance Unit, 1914-1919, a record*, Swarthmore Press, London, 1920, p. 215.]

The bibliographic list in *Flora Malesiana Bulletin* 28 gives 1921 as the year of his earliest publication. In fact, the period of his service in France in the Friends' Ambulance Unit was the scene for his first published article: *Social Life of the Convoy*, pp. 91-95 in Herbert Wright's book cited above, predating all others by two years. It is an interesting note on how he and his colleagues lived in France, and makes light of time that must have been to a very large extent one of tedium, squalor, fear and fortitude. The article shows an amateur theatrical group called 'The Duds', but unfortunately he can not be recognised amongst them.

I am grateful to Mr. Malcolm Thomas of the Society of Friends for his help in finding this information.

Dr. R. E. Holttum — Eightieth Celebration

by

A. C. JERMY

British Museum (Natural History)
London

On 30 July 1975, some 75 friends and colleagues gathered in the Jodrell Laboratory, Royal Botanic Gardens, Kew, England, at the kind invitation of the Director, Professor J. H. Heslop-Harisson, to celebrate the eightieth birthday of Dr. Richard Eric Holttum.

The occasion was organised by a group representing the Linnean Society of London (from which Dr. Holttum was presented with the Linnean Medal in 1964), the British Pteridological Society (of which he was a Past President) and the Royal Botanic Gardens, Kew, at which Holttum spent most of his retired, but hard-working, hours.

After sherry in the Staff Common Room guests assembled in the Lecture Theatre to applaud a number of presentations to Eric Holttum made by distinguished guests on behalf of well-wishers both in England and abroad. Mr. P. M. Brenan, Deputy Director of R. B. G. Kew, representing the Director who was unfortunately abroad, presided over the proceedings. He welcomed the guests and presented Dr. Holttum, on behalf of the Director and staff of Kew, with a picture of *Holttumara* 'Cochineal' painted by Rosemary Lowe from material specially sent from Singapore.

Professor Irene Manton, President of the Linnean Society of London, then presented Dr. Holttum with a portrait of himself drawn by Mrs. Julia Pannett and subscribed to by friends and colleagues in the United Kingdom, Singapore, New Guinea, New Zealand, Holland, Denmark, Switzerland, United States of America, Jamaica, South Africa and India. Professor Manton went on to present him with a special issue of the *Fern Gazette*, the journal of the British Pteridological Society, published on that day in Holttum's honour. It was then the turn of Dr. G. Seidenfaden, formerly Danish Ambassador to Thailand and a well-known orchidologist, who rose to read a statement of good wishes from the President, Mr. Quek Kiah Huat, and Members of the Orchid Society of South-East Asia, and presented Holttum with a gold medal struck by the Society to commemorate his eightieth birthday. Telegrams and letters of good wishes were then read from Mr. A. G. Alphonso, Deputy Commissioner i/c Singapore Botanic Gardens; the Singapore Branch of the Malayan Nature Society; Mr. John Ede, President of the Singapore Gardening Society; and Dr. R. M. Tryon, President of the American Fern Society.

At this point, Mrs. Jean Brenan, presented Mrs. Ursula Holttum with a bouquet of flowers, whereupon Professor C.G.J.J. van Steenis, formerly Director of the Rijksherbarium, Leiden, on behalf of colleagues at Leiden and the Flora Malesiana Foundation, presented Holttum with a live young plant of *Platycerium holttumii* Hennipm. and Joncheere.

The guests had a pleasant walk through the Gardens to the Restaurant where they enjoyed a dinner given in Dr. Holttum's honour. The guest speakers, Mr. Henry Schollick, President of the British Pteridological Society and Professor C.G.J.J. van Steenis gave short but amusing speeches, befitting the informality of this delightful and memorable occasion. Eric Holttum, dressed in a colourful Singapore shirt, replied both to the presentation before dinner and to the salutations of the after-dinner speeches.

Even the English weather celebrated the occasion: a screen temperature of 30°C was recorded that day at Kew.

Guests at Professor Holttum's Birthday Celebrations

30 July 1975

Dr C. D. Adams
Mr G. Black
Dr D. F. Blaxell
Mr & Mrs J. P. M. Brenan
Mr F. H. Brightman
Mr H. J. Bruty
Mr & Mrs J. A. Crabbe
Dr & Mrs J. Croxall
Dr D. F. Cutler
Mr J. W. Dyce
Mr & Mrs P. J. Edwards
Mr L. Forman
Dr & Mrs G. W. Gillett
Dr A. D. Greenwood
Miss Mary Gregory
Mr & Mrs J. W. Grimes
Mr E. Hennipman
Dr & Mrs G. Herklots
Miss D. Holttum
Dr C. Hubbard
Dr M. Jacobs
Dr Frances Jarrett
Mr & Mrs A. C. Jermy
Mr G. J. de Joncheere
Mrs R. Lowe
Dr J. D. Lovis
Mrs MacDougal
Prof. Irene Manton
Mr P. McKenzie Black
Mr W. Marais
Dr & Mrs R. Melville
Dr & Mrs Panigrahi
Mrs J. Pannett
Mrs A. P. Passey
Miss T. K. Power
Dr & Mrs D. A. Reid
Prof. & Mrs P. W. Richards
Dr & Mrs N. Robson
Mr H. Schollick
Dr G. Seidenfaden
Mrs P. Simmonds
Dr Anne Sleep
Dr & Mrs W. T. Stearn
Prof. & Mrs C. G. G. J. van Steenis
Mr P. Taylor
Mr P. Temple
Dr & Mrs B. A. Thomas
Dr J. Vaughan
Dr & Mrs T. G. Walker
Mr P. J. Wanstall
Mr S. L. Williams
Dr & Mrs T. C. Whitmore
Mr & Mrs J. S. Womersley
Mr & Mrs J. Woodhams

Holttum's contribution to horticulture in the Malaysia-Singapore region

by

K. C. CHEANG* and A. G. ALPHONSO**

Horticulture both in Malaysia† and Singapore has taken on a very significant role to-day. With rapid urbanisation the importance of planting trees and garden plants whether for beautification or for other aesthetic reasons, has become not only a very important undertaking, but a way of life with the peoples of the region. Many, both amateurs and professionals, who are involved with gardening and other horticultural pursuits in this region, make constant references to two famous publications — "Gardening in the lowlands of Malaya," and "Flora of Malaya, Vol I — Orchids." The author of these publications is none other than Professor R.E. Holttum. To the amateur who tends his house garden, to the professional gardener who runs a commercial orchid nursery or ornamental garden, to the horticulturists of horticultural establishments, Holttum is a household name. That this should be so is not surprising as Professor Holttum has done more for the promotion of horticulture in this region than anyone else.

Holttum first came out to Singapore in 1922, at a time when there were a few Chinese commercial gardens growing some orchids and a few flowering and foliage plants. Most of these gardens were in Orchard Road, Thomson Road and the Newton and Bukit Timah districts of Singapore, and a few in Penang. Interest in gardening among the people at this time was keen, but there was no proper guidance by an authority on the subject. Holttum befriended the Chinese gardeners, and spent considerable time discussing with them horticultural matters, and at the same time observing the traditional Chinese methods of growing plants, one of which was the use of burnt clay as a potting medium. There was here an interchange of knowledge between the botanist and the practical gardener. A few of these gardeners who are alive to-day and whose children now carry on the management of their nurseries, speak very highly of Holttum, both as a horticulturist and as a kind man. Holttum's knowledge of horticulture was not obtained from books alone. His was a practical approach to the subject as a result of long experience in the growing of tropical plants in the region. He did not as a rule, resort wholly to scientific methods, or put forward scientific suggestions. In the pursuit of gardening, he always made it easy for the ordinary man.

In 1928 Holttum together with John Laycock and Emile Galistan, two very keen orchid growers founded the Malayan Orchid Society. At this time there was a great interest shown by the public in the growing of orchids, and the three must have realised that such a Society would play an important role in the promotion of orchid growing in the country. A few years later the Singapore Gardening Society was formed, and Holttum was mainly responsible for its founding. Meetings were regularly held for members, and the two Societies under the expert guidance and advice of Holttum flourished, and played a great role in the promotion of orchid growing and gardening in the region. Annual shows were held, the first being an orchid show organised by the Malayan Orchid Society (now the Orchid Society of S.E. Asia) on the 27th and 28th of March 1931 at the

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* lately Head, Botanic Gardens, Penang.

** Botanic Gardens, Singapore.

† here denotes Malaya, Sarawak and Sabah.

YMCA Building in Stamford Road, Singapore. Holttum was mainly responsible for putting up the exhibits of the many species of orchids and the newly raised hybrids of the Singapore Botanic Gardens. It was Holttum who for the first time at this exhibition demonstrated to the Singaporeans and Malaysians alike, the Knudson method of asymbiotic flask culture of growing orchids, showing flasks of orchid seeds at the germination stage, others with seedlings at different stages of growth, and finally established seedlings planted on pieces of wood. This technique in orchid propagation, which Holttum started in 1928 was the turning point in the growing of orchids in the Malaysia-Singapore region, and in fact the whole of S. E. Asia. Seeds could now be successfully germinated and as such, was a tremendous asset in the hybridisation and breeding of orchids in the region. Holttum himself produced a large number of hybrids. The orchid shows continued annually until 1934, when the first flower show including both ornamental and orchid plants was held at the New World Stadium from the 6th–8th April, and jointly organised by members of both the Malayan Orchid Society and the Singapore Gardening Society. These shows were to continue annually to the present time. Holttum must have known that horticultural shows are of immense value to both professional and amateur growers, for they serve to raise the standard of horticulture in the country by giving the growers a chance to compare their exhibits and to show what can be achieved. They also help to encourage the non-gardener to take an interest in gardening. Holttum retired as Director of the Singapore Botanic Gardens in 1949 and was appointed Professor of Botany at the newly formed University of Malaya. He held this post until 1954 when he returned to England. For over 25 years he had devoted his time energetically to the activities of the Malayan Orchid Society and the Singapore Gardening Society.

Although the flora of the Malaysia-Singapore area is one of tropical rain forest, it is surprising to note that there are few indigenous plants of horticultural value. Native ornamental plants and flowering trees are few compared to the abundance of species in the flora of the area. The flowering trees and ornamental plants grown in one's garden, in parks and open spaces, by roads and streets and even in the Botanic Gardens, have mostly been introduced especially from Central and South America, and other parts of Tropical Asia. The introduction of new plants into Malaysia and Singapore has therefore played an important role in the horticultural beautification of the area. Although private individuals, business houses and other establishments have to some extent been responsible in the introduction of plants into this region, it was Holttum, during his 27 years of office as Assistant Director and Director of the Gardens Department, Straits Settlements (Singapore, Malacca and Penang), who was mainly responsible for the countless numbers of flowering trees and shrubs introduced to the two Botanic Gardens in Singapore and Penang from tropical regions of North and South America, Africa, Asia and Australia. Many of these plants to-day are extensively grown in parks, by roadsides, and private gardens and commercial nurseries throughout Malaysia and Singapore.

Holttum is a widely travelled person, having attended many international horticultural conferences. His lectures and papers presented at these conferences included topics on various aspects of horticulture in this region, particularly relating to orchids and ferns.

Some thirty odd plants, both species and hybrids, have been named after Holttum. Perhaps the trigeneric orchid hybrid Holttumara cochineal (*Arachnis* x *Renanthera* x *Vanda*) is the most outstanding as far as horticultural plants are concerned. A painting of this hybrid was made by a staff member of the Royal Botanic Gardens, Kew, and presented to Holttum on his 80th birthday. Some years back the authors on a plant collecting trip to Kaki Bukit in Perlis, Peninsula

Malaysia, discovered a staghorn fern which was appropriately named *Platycerium holttumii*, for no one in this region has done more towards popularising the growing of ferns as a decorative house plant than Holttum.

In 1940 for the first time, three local officers were recruited by Holttum for horticultural training. K. C. Cheang was assigned to the Botanic Gardens in Penang, A. G. Alphonso to the Botanic Gardens in Singapore and N. V. Lange to the Parks Department in Singapore and subsequently to the Parks Department in Ipoh, Perak. Holttum must have realised at this time that the future of horticulture in the region rested with qualified local horticulturists. Up to such time horticulturists were expatriate officers recruited from the Royal Botanic Gardens, Kew. Apart from the training received directly under Holttum, the officers were sent to the College of Agriculture in Serdang, Malaysia, and later K. C. Cheang proceeded to Massey University, New Zealand, N. V. Lange to the Institute of Parks Administration, England, and A. G. Alphonso to the Royal Botanic Gardens, Kew. On their return they were appointed Curators, and were subsequently to head their respective departments. It was during the period of training under Holttum that the authors had come to appreciate him as a truly outstanding horticulturist. His immense knowledge of local plants and his long standing experience in practical gardening, won him the admiration of all who came to know and learn under him. Above all, he was a very kind person, and was always willing to help his fellow-men. We are proud and honoured to have served under Holttum.

Holttum's contribution in the field of horticulture has won him many honours and he has been the recipient of a number of awards from horticultural societies in the U.S.A., Great Britain and Singapore. In recognition of his work on orchids in Malaysia and Singapore, Holttum, at the 4th World Orchid Conference held in Singapore in 1963, was awarded the Gold Medal of the Malayan Orchid Society. In addition, the Orchid Society of S.E. Asia awards annually a Gold Medal known as the Eric Holttum Gold Medal to the originator of the best locally produced hybrid. On the occasion of his 80th birthday the Orchid Society of S. E. Asia, at a ceremony at the Royal Botanic Gardens, Kew, presented him with a Gold Medal suitably inscribed, and through the generosity of the Singapore Gardening Society, the Botany Department of the University of Singapore presents annually a Holttum Silver Medal to an honours student who has performed well in his examinations.

Perhaps Holttum's biggest contribution to horticulture in the Malaysia-Singapore region lies in his published works. He is a prolific writer, and his many articles on gardening in the Malayan Agri-Horticultural Association magazine for well over 20 years, are not only instructive but of great benefit to both the amateur and professional gardener. The Malayan Orchid Review, the official organ of the Malayan Orchid Society was first published in 1931. Holttum was the main contributor. He was the expert, and his many and varied topics in the Orchid Review have helped orchid growing in this region. By far, his best works in horticulture and by which the Malaysian and Singaporean will best remember him, are his "Gardening in the Lowlands of Malaya" and his "Flora of Malaya, Vol I — Orchids", mentioned earlier. The former is an excellent book on practical gardening in this region. It is as popular to-day as when it was first published in 1953. The latter, the most outstanding publication on orchids of this area, has been a constant companion of the orchid growers. Holttum is also the author of many other publications on local plants of horticultural interest. His "Flora of Malaya, Vol II — Ferns" and articles on Bamboos, Gingers, Maranta, Grasses and others, published in the Gardens' Bulletin, although taxonomic or botanical in nature, have in many ways helped the horticulturist in his work, especially in the identification of plants he deals with.

We in this region owe a debt of gratitude to Holttum for his outstanding contribution to horticulture. To-day, in both Malaysia and Singapore, there is a thriving orchid industry. The value of present exports of cut orchid blooms from both these countries has reached nearly ten million local dollars. Orchid nurseries have come up in large numbers, and there is no doubt that the orchid industry will continue to expand. This situation would not have come about had it not been for the pioneer work of Holttum in orchid growing. His introduction of asymbiotic flask culture of orchids n 1928, the breeding and hybridisation of orchids which he started, and the encouragement he gave to professionals and amateurs in the field of horticulture have borne fruit.

The role he played as adviser to the Parks Department and in the planting of roadside trees in the early years, his able administration of the two Botanic Gardens of Singapore and Penang, and the valuable knowledge he has imparted to the students as Professor of Botany at the University of Malaya, bear testimony to his foresight and vast horticultural knowledge. And above all, his many horticultural publications will be constant reminders to us all of his dedicated service in this region.

This number of the Gardens' Bulletin is specially brought out to commemorate the 80th birthday of Professor Holttum, and in writing this article the authors join the many Malaysians and Singaporeans, the orchid growers, the amateur and professional gardeners, and the members of the Orchid Society of S. E. Asia and the Singapore Gardening Society, in wishing him good health and happiness in the years ahead.

Staghorn Ferns Today and Tomorrow

by

Barbara Joe HOSHIZAKI

Botanical Gardens-Herbarium
University of California
Los Angeles

The unique appearance of staghorn ferns (*Platycerium*) has attracted the attention of enthusiasts for well over a hundred years. Modern transportation and communication have brought all 18 species into cultivation. So great is interest in this fascinating fern group that it seems appropriate to note recent horticultural and botanical works that have solved many puzzles and to look ahead to problems yet to be answered.

Horticultural contributions. Horticultural interest in staghorn ferns has greatly benefited botanical work. The perseverence and tenacity of *Platycerium* fanciers who seek out new plants, grow them, and develop new varieties is amazing. Through their efforts I have been able to study every one of the known Platycerium species as live plants. The opportunity to watch plants grow from spore to maturity contributed greatly to the botanical knowledge of the genus.

Platycerium enthusiasts in United States cultivated a new species from Malaysia for several years before it was recognized and named by botanists (Joncheere and Hennipman 1970). This handsome plant, now called *Platycerium holttumii,* was well known enough by amateurs to have been photographed for two popular books prior to being formally named (Rüe et all 1957, Franks 1969). A second new species, the *P. grande* of the Philippines, has been recognized in the last few years (Joncheere and Hennipman 1970), another exciting event to platycerium fanciers! These relatively recent discoveries kindle the imagination of collectors who hope that different species may still be discovered. Collectors continue their quest for new and unusual platyceriums. Shipments of *P. wallichii* have reappeared in the United States, and these plants do show some frond variation. The significance of these variations has yet to be investigated. These plants were reported to have been collected along the India-Burma border. Native plants of *P. stemaria* have an interesting range of frond variation which may interest botanist as well (Joe 1964). But besides seeking variations among wild plants, horticulturist are developing new garden varieties. The multititude of new garden varieties is due to the increased number of people raising plants from spores. A hybrid platycerium, *P. mentelosii* (*P. stemaria* x *superbum*) has been developed and other hybrid combinations will most likely follow (Hoshizaki 1975). Growers tell us that platyceriums are quite plastic in their leaf form. Slight changes in the environment may cause base fronds to become partly foliaceous, normally entire fronds to become forked and so forth.

Staghorn fern propagation by meristem or tissue culture is being actively investigated by commercial nurseries. They claim that plants may grow twice as fast through meristem culture as by spores. Meristem plants tend to produce mutations more frequently than spore grown ones and this interest horticulturist and geneticist.

The Malaysian plant, *Platycerium ridleyi,* thought extinct, has been found and introduced into United States cultivation. It grows very nicely in southern California greenhouses if adequately protected from slugs and snails. Spores from these introduced plants have produced mature plants, thus insuring the species' survival and reducing the need to collect these rare plants from native habitats, a happy circumstance for conservationists.

Much more information is needed on the cultural conditions for *Platycerium wallichii* of Southeast Asia, and *P. madagascariense* and *P. quadridichotomum* both of Malagasy. These species, being difficult to cultivate, create demands for replacement, a situation which is not encouraging for conservationists. Hopefully more work along the lines of Boyer will help in the successful growth and propagation of these plants. Boyer closely examined the ecology, physiology, and mineral needs of two African species, *P. angolense* and *P. stemaria* (Boyer 1964).

The type of foregoing activities and results generated by horticulturists hold promise of supporting and even giving direction to scientific work and increasing our understanding of the genus. To help science, horticulturist should be encouraged to maintain reliable records as to where native plants were collected, or if new plants were developed in cultivation, the names of the parent or parents involved. Conditions which may have caused unusual growth patterns should also be recorded. Horticulturists on the other hand should protect native plants and prevent their extinction from indiscriminate collecting.

BOTANICAL CONTRIBUTIONS. The name changes among platycerium species confuse and frustrate growers and most botanists. If it is any comfort to know, botanist specializing in nomenclature have for years been trying to unravel the technical complexities in determining the proper name for certain species. A series of papers and rebuttals dealing with this problem has been published in the last few years by G. J. Joncheere and the late C. V. Morton (Morton 1964, 1970, Joncheere 1967, 1974). The main issues first center around whether *Platycerium vassei* as conceived by botanist, not horticulturist should be called *P. alcicorne* and second, whether *P. angolense* should be called *P. elephantosis*. A few botanist are following this intricate and complicated problem and their views will be forthcoming. Morton's argument, that the correct spelling of *P. stemaria* is not *P. stemmaria, seems* to be upheld. The acceptance of *P. wandae* as the legitimate name over *P. wilhelminae-reginae-* seems without complication (Joncheere 1968). However, among plants introduced from New Guinea and now growing at Longwood Garden, Pennsylvania are two kinds of *P. wandae*. One produces long fertile fronds fitting the original description of *P. wilhelminae-reginae* and the other produces short fronds closely fitting the description of *P. wandae*. In all likelihood both plants are one species. Short and long fertile frond forms have also been noted in *P. coronarium*. However, further study and field observations on long and short frond plants might be of interest.

It is indeed unfortunate that the name *Platycerium grande* must now be applied to the Philippine plant instead of the Australian plant. The Australian plant must now be called *P. superbum* in accord with Joncheere and Hennipman (1970). I examined the rhizome scales of the Philippine plant and they differ from the Australian plant, though both are closely related. Rhizome scales of the Philippine plant are very similar to *P. holttumii* except for having slightly fewer cells in the marginal hairs (highest number of cells in the longest hairs were mostly 7 in *P. grande* and 8 in *P. holttumii*). The scale morphology is consistent with other morphological data which relates *P. grande, P. superbum,* and *P. holttumii* (Hoshizaki 1970, 1972).

The relationships of the Australian-Javan species (*Platycerium bifurcatum, P. veitchii, P. willinckii,* and *P. hillii*) and their distribution still needs to be clarified with more data. Some of the features separating these supposedly different species are not stable from observations on plants in cultivation. Mr. Ernest Todd of New South Wales, Australia has been investigating the distribution of the Australian-Javan species. In a personal communication Mr. Todd reports that the collections of

P. bifurcatum by Bambler and others in New Guinea were probably taken from cultivated or escaped plants most likely introduced by German missionaries in the early part of the century. Distributions of some of the Malayan-Asiatic species also need further clarification.

Platycerium coronarium and *P. ridleyi* are very closely related species, yet there is a gap between these two species and their closest relatives. It doesn't seem too far-fetched to speculate that some yet undiscovered species may be found in the Malaysian area that bridges this gap and others as well.

With the relatively wide-spread use of the scanning microscope studies should be encouraged on the ontogeny of stellate hairs in this genus and its proposed relatives (*Pyrrosia* and *Drymoglossum*). It might be worthwhile to also study and compare these genera as to sporangial structure. Within the platyceriums are species with complete to incomplete annular rings, laterally and apically located lip cells, and stalk structure variations.

Certainly there are many topics I have not touched upon that should be considered in future studies. However, I want to stress that botanist and horticulturist have much to look forward to in knowing more about these unusual plants.

Literature cited

Boyer, Yvette née Menoux. 1964. Contribution a l'estude de l'ecophysiologie de deux fougeres epiphytes: Platycerium stemaria (Beauv.) Desv. et P. angolense Welw. Théses présentées a la Faculté des Sciences de l'Universite de Paris. Série A, No. 4191, No. d'ordre: 5042.

Franks, Wendy. 1969. *Platycerium Fern Facts*. Privately published. 119 p.

Hoshizaki, Barbara Joe. 1970. The Rhizome Scales of Platycerium. *Am. Fern J.* **60**: 144–160.

Hoshizaki, Barbara Joe. 1972. Morphology and Phylogeny of Platycerium Species. *Biotropica* **4**: 93–117.

Hoshizaki, Barbara Joe. 1975. A Staghorn Fern (Platycerium) Hybrid. *Am. Fern J.* **65**: 99–101.

Joe, Barbara. 1964. A Review of the Species of Platycerium (Polypodiaceae). *Baileya* **12**: 69–124.

Joncheere, G. J. de. 1967. Notes on Platycerium Desv. I. Nomenclature and typification of the genus and species in Desvaux's original publication of 1827. *Blumea* **15**: 441-451.

Joncheere, G. J. de. 1968. Notes on Platycerium Desv. II. P. wilhelminae-reginae v.A.v.R. reduced to P. wandae Rac. *Blumea* **16**: 109–114.

Joncheere, G. J. de. 1974. Nomenclatural notes on Platycerium (Filices) *Blumea* **22**: 53–55.

Joncheere, G. J. de and E. Hennipman. 1970. Two new species of Platycerium and the identification of P. grande (Fee) Presl. *Br. Fern Gazette* **10**: 113–118.

Morton, C. V. 1964. The Nomenclature of a Madagascarian Platycerium. *Baileya* **12**: 36–38.

Morton, C. V. 1970. A further note on the type of Platycerium alcicorne. *Am. Fern* J. **60**: 7–12.

Rüe, Edgar Aubert de la, Francois Bourlière, Jean Paul Harroy. 1957. *The Tropics*. Knopf. 208p.

A new species of Nastus Nees (Gramineae) from Sumba

by

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Summary

An illustrated description of *Nastus reholttumianus* S. Soenarko is presented and this new species is compared with *N. rudimentifer* Holtt. and *N. obtosus* Holtt.

When Holttum (1956) transferred the Malesian species of *Oreiostachys* Gamble to *Nastus* Nees, three species of *Nastus* were known from New Guinea. In 1967 he described four more species and Bor (1972) added one to these; thus there are now eight species endemic to New Guinea. Outside New Guinea there is one species; it occurs in Java.

In most of the Malesian *Nastus* the spikelets are more or less cylindrical, thus the fourth and the fifth glumes, lemma and palea are rounded at the back (except those in *N. schlechteri* (Pilger) Holtt., in which they are more or less 1-keeled), with usually prominent nerves; moreover the palea is bifid. A plant collected by Mr. Iboet from the island of Sumba (Indonesia) has characteristically small and laterally compressed spikelets, lightly 1-keeled glumes, lemma and palea, with prominent middle nerve and several (usually 6) faintly lateral nerves, and acuminate palea. These structures, together with the leaf size (up to 8 cm long and 14 mm wide) differentiate the Sumba plant from the other Malesian *Nastus*, and it is regarded here as a new species, *N. reholttumianus*. The near relatives of this new *Nastus* are *N. rudimentifer* Holtt. and *N. obtusus* Holtt. which have similar panicle with spreading branches and short-tipped lower glumes. However, this new species differs in several respects from the two latter; their characters are compared in the table below:

characters	reholttumianus	rudimentifer	obtusus
leaf-blade of flowering branch	4.5-8 cm long 7-14 mm wide	(8) 10-12 cm long 15-27 mm wide	12-15 cm long 12-15 mm wide
spikelet	± laterally compressed 5-7 mm long	± cylindrical 12 mm long	± cylindrical 13-20 mm long
rachilla extension	absent	present, sometimes absent	usually absent
lemma	6 mm long, glabrous	10 mm long, glabrous	14-17 mm long, with appressed hairs on the back
palea	acuminate	bifid	bifid

Nastus reholttumianus S. Soenarko, *sp. nov., N. rudimentifer* Holtt. affinis sed spiculis 5 – 7 mm longis, latere compressis, lemmate 6 mm longo, lamina 8 longa differt. TYPUS: Sumba, *Iboet 443* (holotypus, BO).

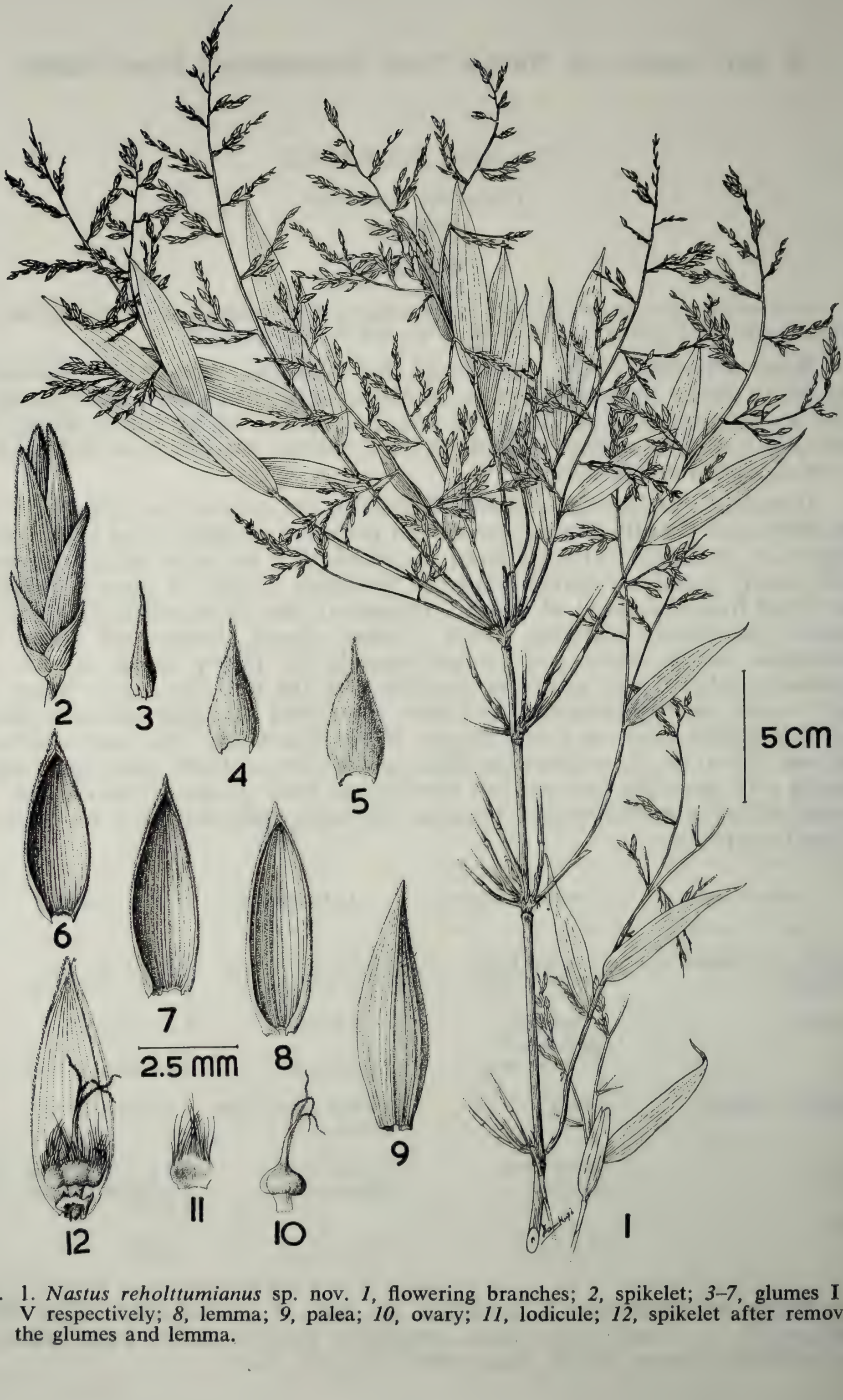

Fig. 1. *Nastus reholttumianus* sp. nov. *1*, flowering branches; *2*, spikelet; *3–7*, glumes I — V respectively; *8*, lemma; *9*, palea; *10*, ovary; *11*, lodicule; *12*, spikelet after removing the glumes and lemma.

Culm not seen, upper part bearing flowering branches 3.5 mm diam., either solid or hollow, with annular woody ring below each node; branches glabrous, 3–8 in each node. Culm-sheath not seen. Flowering branch 11–22 cm long; leaf-blades 4.5–8 cm long, 7–14 mm wide, oblong-lanceolate, glabrous, acuminate, rounded at the base; leaf-sheath glabrous; ligule less than 1 mm long; auricle up to 1 mm long, fringed (fringe 1–2 mm long). Inflorescence open panicle with spreading branches, main axis and branches with minute appressed hairs. Spikelet more or less laterally compressed, up to 7 mm long, glabrous; glume I: 1.5 mm long, narrowly ovate, 1-keeled on the back, with mucronate apex; glume II: 2.5 mm ovate, slightly 1-keeled on the back, mucronate; glume III: 3.5 mm long, slightly 1-keeled on the back, ovate, faintly 6-nerved with conspicuous median nerve (and so are the median nerves of glumes I and II); glume IV: 5.5 mm long, ovate to ovate-oblong, boat-shaped, acuminate, 3 mm wide, faintly 7-nerved; glume V: more or less similar to glume IV, but slightly longer; lemma and palea more or less equal, 6 mm long, ovate-oblong, acuminate, boat-shaped to slightly compressed; lodicule 1 mm long with fringes; ovary stalked with conical fleshy apex, glabrous, the stalk often elongates up to 2 mm long; rachilla extension absent; stamens 6, anthers 2.5 mm long. (Fig. 1).

Sumba. Mangiliwari near Maomaru, 9. V. 1925, *Iboet 443* (BO, holo).

The author dedicates this new species to Prof. R. E. Holttum who has contributed so much to the knowledge of S. E. Asian bamboos, especially of Malaya and New Guinea, and has encouraged the author in studying Malesian bamboos. Thanks are due to Sdr. Damhuri (Herbarium Bogoriense) for preparing the figures.

References

Bor, N. L. (1972). A new species of *Nastus* from New Guinea. Öst. Bot. Z. **120**: 87–91.

Holttum, R. E. (1956). The bamboo-genera *Nastus* and *Chloothamnus*. Kew. Bull. **10**: 591–594.

———— (1967). The bamboos of New Guinea. Kew Bull. **21**: 263–292.

On Iridescent Plants

by

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Abstract

Plants with leaves of iridescent blue and green colour are common in the deep shade of Malaysian rain-forests. Simple anatomical observations have revealed that the green iridescence is due to the refraction of diffuse light onto specially-oriented chloroplasts by lense-shaped cells. Blue iridescence colour is due to the operation of thin film interference filters in or on the epidermis. The advantage of such a filter in forest shade plants is the effective absorption of red wavelengths of light at the expense of the reflection of less important blue wavelengths. This report documents iridescence in the leaves of many unstudied taxa (mainly pteridophytes), common in Malaysian rain-forests.

Life in a tropical rain-forest is not quite as easy for green plants as popular accounts would indicate. First by, the forest soils are generally rather sterile. Secondly, plants are under intense pressure of predation by insects and other animals. Finally, the light conditions are frequently less than optimum—from very bright conditions in the canopy to deep shade on the rain-forest floor. In this discussion we are concerned with the deficiency of light in the shade at the bottom of the rain-forest; in this environment can be seen a number of plants whose leaves display brilliant blue and green colours. These colours can be described as *iridescent* because of their intensity and metallic quality. The association of these iridescent plants with the shady and moist environments has compelled many naturalists to reason that the colours must be associated with adaptations which help the plants to survive in the dark habitats. The rain-forest floor is one of the darkest environments in which plants grow. Not only is the total light quantity a small fraction of that above (less than one percent) but also the light quality is diminished; more of the wavelengths vital to photosynthesis, with the exception of some red light, have been absorbed by the foliage overhead (Evans, 1966; Federer and Tanner, 1966; Bjorkman, 1972). The purpose of this discussion is to explore how the iridescence of some Malaysian plants is associated with adaptations to increase the absorbance of diffuse and weak light for maximum photosynthetic efficiency.

LEAF ANATOMY AND FUNCTION

Leaves possess many structures which are significant in the efficient absorption of light in shady environments (see Ray, 1972; and Esau, 1965). Figure 1 summarizes these structures.

The Cuticle. The function of the cuticle is two-fold (see Martin and Juniper 1970 for further details). First, it repels water and prevents the rapid dessication of the leaf. Secondly, it can act as a selective filter in reflecting harmful ultraviolet light, and allowing the absorption of visible light essential for photosynthesis.

The Epidermis. This superficial cell layer, particularly on the upper leaf surface, may possess special adaptations for efficient light absorption. It may have bumps which remain dry when the lower areas are covered by rainwater; these allow more efficient light absorption in wet conditions (Haberlandt, 1914).

Epidermal cells may also have regularly convexly curving upper surfaces; these focus diffuse sunlight onto specially orientated chloroplasts. Finally, the epidermal cells of extremely shade-tolerant plants (especially pteridophytes) may contain chloroplasts which can more directly receive light before it is scattered by the cell walls.

Photosynthetic Parenchyma. Both the palisade and spongy mesophyll layers may have special adaptations for low light environments. They may be specially oriented beneath the lens-like epidermal cells. In shade-tolerant plants these cells would have fewer and larger chloroplasts. The protein/chlorophyll ratio, which reflects the relative plant investment in light reception versus biosynthetic apparatus, would be low. Finally, the cells may be closely packed together to minimize the reflection (and loss) of light between the cells.

Stomata. In low light environments the stomata will not be a limiting factor, and we might expect various arrangements on the upper and, especially, lower leaf surfaces.

Leaf Size and Shape. In low light environments leaves tend to be large and thin, with a high surface/volume ratio. This ratio is increased even more in plants, as ferns, with highly divided leaves.

Thus, the task in understanding the significance of iridescence in shade-tolerant plants is to explain how some attributes of leaf structure confer an advantage on the plants and, at the same time, physically account for the iridescent colour.

IRIDESCENCE

Many plants from diverse taxonomic groups, from humid rain-forests throughout the tropics, possess iridescent leaves (Richards, 1952). Iridescent plants can be observed in Malaysian rain-forests (see Table 1), and some are extremely common. *Selaginella willdenowii* is a scandent pteridophyte frequently encountered in rain-forests, plantations and belukar throughout Southeast Asia. Another pteridophyte, *Athyrium crenatoserratum,* can be frequently observed in local rain-forest, as is *Phyllagathis rotundifolia* (Melastomataceae). Blue-leaved sedges of the genus *Mapania* commonly grow in Sarawak rain-forests. Others are less common. The two kinds of iridescence observed in these plants, green and blue, are discussed separately below.

Green Iridescence. The first observations on green iridescence were made on the cave moss, *Schistostega,* which grows in caves and other dark and wet environments in Europe and North America. Richards (1932) reported that the brilliant green colour encountered at particular angles was due to the functioning of certain protonemal cells as refractive lenses, focussing the diffuse light onto the specially oriented chloroplasts. Analysis of Malaysian green iridescent plants indicates that the same principles operate (see Figure 2 and Plate 1). These plants all share cells (epidermal or palisade) whose outer walls have a uniform convex curve. The chloroplasts are always oriented at the distal end of these cells. When we look at these plants the intense green colour can be observed only at an angle perpendicular to the surface of the plant. At other angles the colour is dull green or even whitish. This effect is due to the focusing of the diffuse light into a more intense beam directly onto the chloroplasts. These organelles, with their parallel stromal organization, absorb the light useful in photosynthesis and reflect the unused green light directly out of the long cells. Thus when we look at these plants, as at the entrance to Batu Caves near Kuala Lumpur or on rocks in especially shady forest habitats, we see the green light reflected in an intense and narrow beam. At other angles the light appearance of the leaves is due to reflection of whole light off of the cell surface acute angles and also the scattering of light within the cells. The birefringence of the cellulosic walls may also be a factor affecting the quality of the light reflected at acute angles.

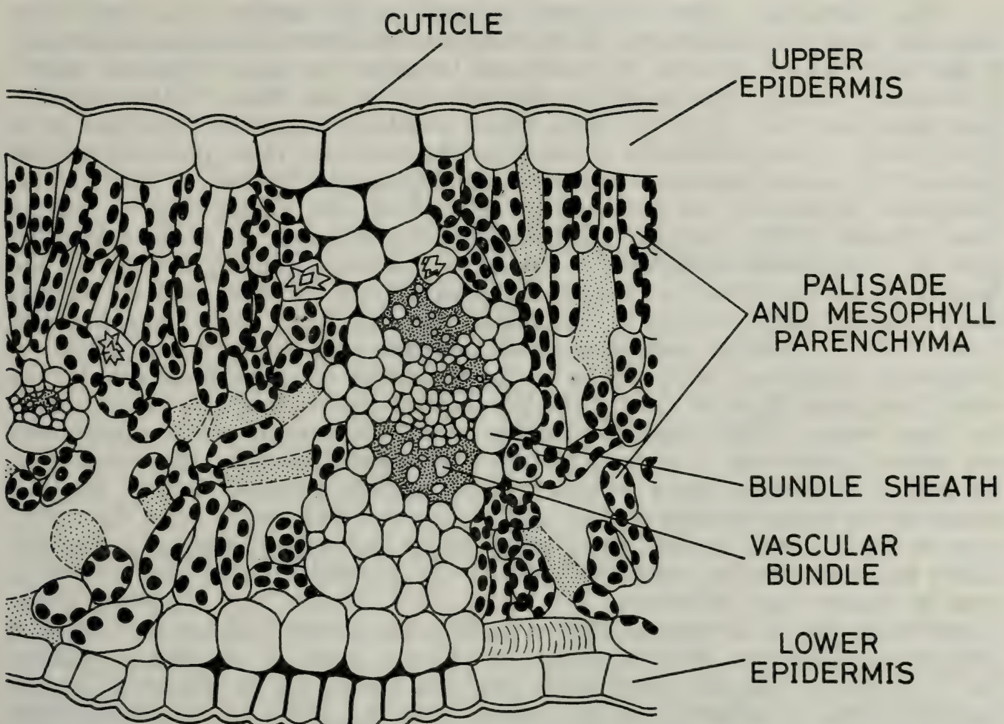
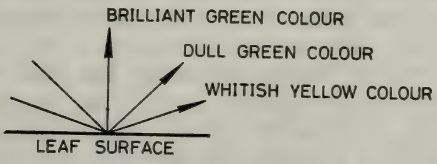


Fig. 1. A diagram of the typical structure of a leaf.



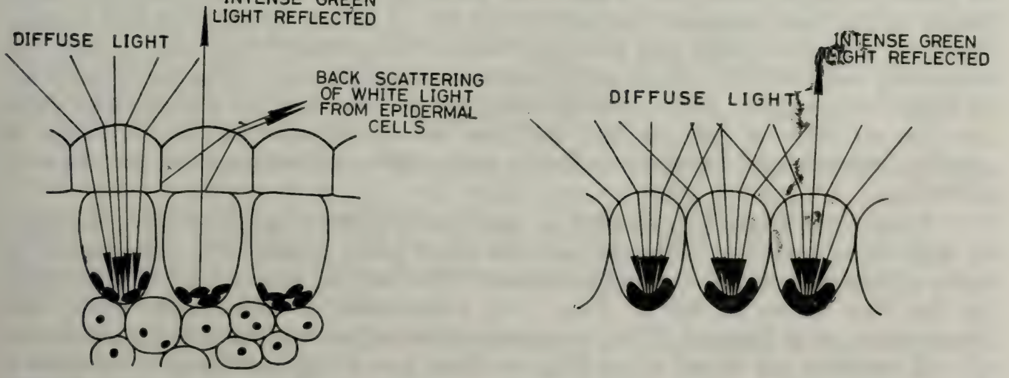


Fig. 2. The mechanism for the production of green light in iridescent green plants.

Blue Iridescence. Men have been intrigued by the startling blue plants ever since they were first encountered. In the Malaysian rain-forest *Selaginella willdenowii* is the most striking example. In traditional languages the name "peacock plant" is frequently used to describe these pteridophytes (as the Malay "paku merak"). One aboriginal Senoi name for these plants translates roughly as "the hair on a tiger's rump" (Gerard Diffloth, personal communication). These plants have been included in various medicinal remedies probably simply because of their colour. *Selaginella willdenowii* has been used in preparations for aching back as well as fever (Burkill, 1935). European scientists made frequent mention of the colour but gave no explanation. Stahl (1896) studied *S. willdenowii* while working in the famous Treub Laboratory at Bogor. He observed that the iridescent colour was due to pigmentation granules in the cuticle. Fox and Wells (1971) and Lee and Lowry (1975) recently published more adequate explanations for colour in *Selaginella willdenowii*, likely also to be the mechanism of colour formation for the other blue plants listed in Table 1. Stahl's original observations can be discounted for three reasons. There are no presently known pigments in pteridophytes with the spectral properties to account for the blue colour. Secondly, in re-examining the epidermis of these plants we observed no pigment granules. Thirdly, the blue colour of the leaves disappears when they are covered with water. Thus, the colour must be due to some physical optical effect of the leaf surface, and not a pigment. There are three physical phenomena which can account for iridescent colour as seen in insects (see Michelson, 1911; Fox, 1959; Neville and Caveney, 1969). These could also be invoked to explain the blue leaf colour. Diffraction of light on thin gratings disperses different colours at different angles to the object's surface. In *S. willdenowii* and the other plants, only blue colour can be observed. Tyndall scattering (which explains blue sky colour) polarizes light; no polarizing effects have yet been observed in any iridescent plants. Light interference, due to thin films, can produce uniform colours over relatively wide angles of incidence, and is the likely physical explanation of the phenomenon.

The principle of a thin film (or quarter wavelength) interference filter is not familiar to most biologists, and requires some explanation. As a specific example, if the conditions described in Figure 3 are met, optical interference will result in the differential absorbance and reflection of different wavelengths of light. First, the filter must have a slightly different refractive index (r) than the surrounding medium, the air above or the cell below. Secondly, the filter must be exceedingly thin, a fraction of the wavelength of visible light. Thus, in the filter described in Figure 3, the thickness (142μ) is fraction of red visible light at 600 μ. If we trace the path of blue light (at 405 μ) through this filter, we see that light of this wavelength will be reflected by the filter. The distance travelled from A and back to C equals the wavelength of that light in the filter. Retarding the light by one wavelength puts the light (visualized as a transverse wave) in phase, and the energy at this wavelength moves out of the filter. However, light with four times the wavelength of the filter thickness (or red light of 795 μ) would be retarded half a wavelength at the same point, and its energy would be nullified. Thus such a filter can selectively enhance the reflection of certain wavelengths and allow the absorbance of other wavelengths. Two common examples are the rainbow colours seen from the thin oil films on rain puddles, and also the special anti-reflection coatings on quality cameras and binoculars. For a more technical explanation see Vasicek (1960).

To test the above hypothesis Lee and Lowry (1975) analyzed the reflectance of light from both the iridescent and the older green leaves of *S. willdenowii* by using a slightly modified spectrophotometer. The analysis gave a peak of reflectance by the blue leaves at 405 μ. They then constructed a filter model fitting this observation, as in Fgure 3. They assumed a filter refractive index slightly in excess of cell contents (of about r = 1.35), or about r = 1.4 as in Figure 3. In such a filter a concellation of the reflection effects would be observed at about 530 μ,

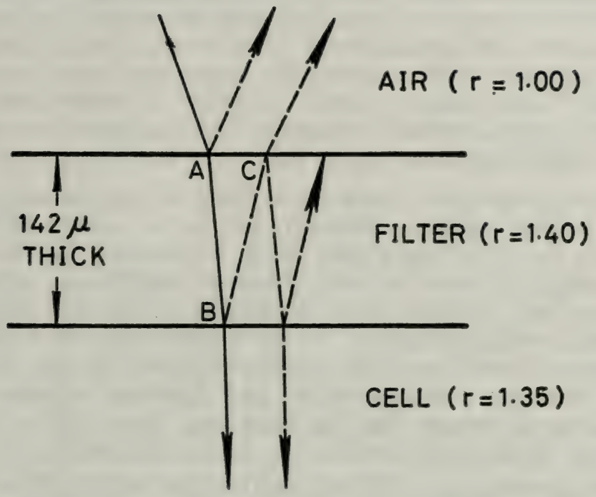


Fig. 3. Operation of a simple thin film interference filter.

1. REFLECTS BLUE LIGHT.

IN THE FILTER, AT AN EFFECTIVE WAVELENGTH OF 284 μ, THE LIGHT IS DELAYED ½ WAVELENGTH AT POINT *B* AND IS NULLIFIED — CANCELLED AS OVERLAPPING TRANSVERSE WAVES WOULD SHOW. AT POINT *C* LIGHT IS DELAYED A FULL WAVELENGTH AND IS REFLECTED OUT — WAVES COINCIDE. AT THIS POINT THE REFLECTED LIGHT HAS A WAVELENGTH OF 405 μ (1.4/1.0 x 284) AND IS BLUE.

2. NO EFFECT ON LIGHT AT 530 μ

AT 2⅔ THE FILTER THICKNESS THE WAVES WOULD CANCEL.

3. ABSORBS RED LIGHT.

IN THE FILTER LIGHT AT A WAVELENGTH of 568μ IS DELAYED ½ WAVELENGTH AT *C* AND IS NULLIFIED — CANCELLED AS OVERLAPPING TRANSVERSE WAVES WOULD SHOW. THUS MORE OF THIS LIGHT PASSES THROUGH THE FILTER AT *B*. HERE THE EFFECTIVE WAVELENGTH IN AIR IS 795 μ (568 x 1.4/1.0) AND IS RED.

with increased absorbance at higher wavelengths. In the difference spectrum obtained by subtracting values of the green leaves from the blue leaves; a curve similar to that predicted was observed (see Figure 4). Light above 700 μ would be reflected by all leaves (Gaussman and Allan, 1973; Gates *et al.*, 1965) and would obscure the filter effect at greater wavelengths. Thus, we have good physical evidence that such filters operate in the blue plants.

The operation of such a filter has obvious adaptive significance for these shade-tolerant plants. Blue light (of which there is little in the dim light of the forest floor) is reflected, and the red light, which is more significant in the total photosynthesis by these plants, is absorbed. Thus, these filters can operate as "anti-reflection" coatings which increase the absorption of photosynthetically active light on the shady forest floor.

Selaginella willdenowii plants possess additional adaptations to increase photosynthetic efficiency. Firstly, the epidermal cells contain single large chloroplasts at the distal ends of the cells (see Plate 2). Thus, most of the photosynthesis occurs just below the leaf surface. Secondly, the epidermal cells have regularly convexly curved surfaces which appear to focus light onto the specially oriented chloroplasts, as previously described for the iridescent green plants. Finally, the iridescent leaves have protein/chlorophyll ratios significantly lower than those exposed to the sun (Krishnan, 1975). These plants possess a number of remarkable adaptations for the improvement of photosynthetic efficiency. The analogy of a camera with coated lenses and high speed film seems apt in describing the function of these plants.

The other blue plants (see Table 1 and Plate 2) are different from *Selaginella willdenowii* in several details, although the same colour-producing principle probably operates for all of the plants. In *S. willdenowii* the blue colour can be removed by dipping the plants in water (blueness reappearing after drying). Other plants do not lose their blueness upon immersion. In the first case, the filter must be in some contact with the surface. In the second case the filter is likely to be found within the cell wall, and not directly exposed to the air. Scans of leaf reflectance for *Athyrium crenatoserratum* and *Lindsaea scandens* are similar to *Selaginella willdenowii,* except that the blue peak is at 410 μ in *Lindsaea* and 415 μ in *Athyrium.* In both of the flowering species observed, *Phyllagathis rotundifolia* and *Begonia pavonina,* I could not ascertain the wavelength of the blue colour because the colour was effectively produced when the incoming light was at a smaller angle to the surface than the reflected light. The method of measurement required a fixed incident angle of 60° for both. The physical constitution of the filters is not presently known, but in all cases the colour is due to a physical optical effect and not to a pigment.

Other blue plants possess distinct anatomical features in addition to *Selaginella willdenowii.* In *Athyrium crenatoserratum* (Plate 2), the epidermal cells also contain chloroplasts, and the outer wall has the convex curve described above. The blue colour is particularly apparent in the older leaves of this common fern. Perhaps the most spectacular iridescent blue plant of all is the rare begonia, *Begonia pavonina.* When looking directly at these plants one sees an intense dark blue colour. However, if the angle of observation is changed so that light is reflected at a more acute angle, the colour changes from blue to dull green and then to gold. An interference filter would account for the blue colour, and the gold colour is probably due to the refractive properties of the epidermal cells. The plant is now under further study. The chloroplasts of *Begonia pavonina* are at the bottom of the palisade parenchyma cells. Both light refraction and interference appear to enhance light absorption in this plant, as in *Selaginella.* The palisade cells are packed very closely together to minimize light loss due to scattering effects. Immediately beneath is a compact mesophyll layer, the cytoplasms of which is dark red with anthocyanins. This layer probably reflects red light (comparatively more abundant on the rain-forest floor) right back up to the chloroplasts in the palisade cells. Thus the *Begonia pavonina* plants appear to have leaves with lenses, filters and special mirrors—all to increase conversion of precious light energy to sugars in the shady forest environment.

FURTHER RESEARCH

Rain-forest floor plants, as in Malaysia, have some spectacular adaptations for the efficient utilization of light. Further studies may uncover new principles, and will help illuminate the functional significance of anatomical details of leaf structure. I see some specific areas of research potential.

First, although there is now some evidence for the operation of thin film interference filters in plants, no one has yet been able to elucidate the structural basis of the filter in the different plants. Lee and Lowry (1975) discounted the

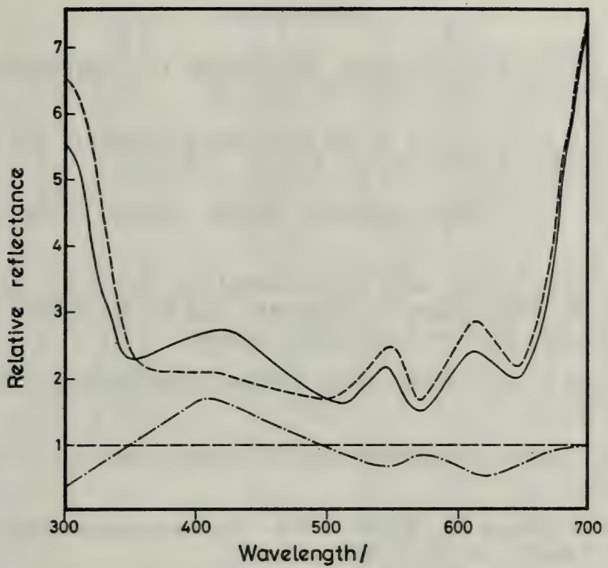


Fig. 4. The relative reflectance of light by green (— — — — — — —) and blue (————————) *Selaginella* leaves as recorded by a spectrophotometer. The bottom curve (—·—·—·—·—·) is the difference between the two curves above and gives a plot similar to that expected for a thin film interference filter.

cuticle as being the molecular basis of the filter in *S. willdenowii;* non-polar solvents, which dissolve cuticle waxes, did not remove the interference. Fox and Wells (1971) speculated that the structural basis for the optical effect may be the trapping of thin layers of air by the epidermis, as is well known for some insects. Critical experimental support for the optical phenomenon of interference should include physical information on the nature—including the thickness and refractive index—of the filter. The small dimensions will necessitate the use of sophisticated electron microscope techniques. If the thickness and refractive index of the filters were known, then we could precisely predict the nature of the interference effect. The basis for the filter may well lie in the orientation of cellulose microfibrils in the cell wall; further research will solve this problem.

Rather esoteric studies on the leaves of shade-tolerant plants may eventually be of some practical importance. In designing more efficient plantation agriculture systems for the tropics, biologists will have to consider the kinds of plants to grow in the understoreys of the plantations. Knowledge of leaf structure may help us select plants which could thrive in such environments. Who knows? maybe someday we will spray interference filters onto the leaf surface of understorey plants, making them blue—and more productive.

Acknowledgements

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References

Bjorkman, O. 1972. Photosynthetic adaptation to contrasting light climates. Carnegie Institution Year Book **71**: 82–135.

Burkill, I. H. 1935. A dictionary of the economic products of the Malay Peninsula, two vols. London, Crown Agents for the Colonies.

Esau, Katherine. 1965. Plant anatomy, second edition. John Wiley and Sons, New York.

Evans, G. C. 1966. Model and measurement in the study of woodland light climates. In R. Bainbridge, G. C. Evans and O. Rackham, eds. Light as an ecological factor. Blackwell Scientific, Oxford.

Federer, C. A. and L. B. Tanner. 1966. Spectral distribution of light in the forest. Ecol. **47**: 555–560.

Fox, D. L. 1953. Animal biochromes and structural colours. Cambridge University Press, London.

———— and James R. Wells. 1971. Schemochromic blue-leaf surfaces of *Selaginella.* Amer. Fern. Jour. **61**: 137–139.

Gates, D. W., H. J. Keegan, J. C. Schleter and V. R. Weidner. 1965. Spectral properties of plants. Applied optics **4**: 11–20.

Gausman, H. W. and W. A. Allen. 1973. Optical parameters of leaves of 50 plant species. Plant Physiol. **52**: 57–62.

Haberlandt, G. 1914. Physiological plant anatomy. MacMillan and Company, London.

Krishnan, Jayamohan. 1975. Physiological leaf anatomy of *Selaginella.* B.Sc. Honours Thesis in Botany, Faculty of Science, University of Malaya, Kuala Lumpur.

Lee, D. W. and J. B. Lowry. 1975. Physical basis and ecological significance of iridescence in blue plants. Nature **254**: 50–51.

Martin, J. T. and B. E. Juniper. 1970. The cuticles of plants. Edward Arnold, London.

Michelson, A. A. 1911. On metallic colouring in birds and insects. Phil. Mag. **21**: 554–567.

Neville, A. C. and S. Caveney. 1969. Scarabaeoid beetle exocuticle as an optical analogue of cholesteric liquid crystals. Biol. Rev. **44**: 531–562.

Ray, Peter, M. 1972. The living plant. Holt, Rinehart and Winston, New York.

Richards, P. W. 1932. The ecology of bryophytes. In Fr. Verdoorn, ed.: Manual of bryology. Martinus Nijhoff, The Hague.

———— 1952. The tropical rainforest. Cambridge University Press, London.

Stahl, E. 1896. Uber Bunte Labblatter. Ein Beitrag zur Pflanzenbiologie II. Ann. Jard. Bot. Buitenzorg **13**: 137–216.

Vasicek, A. 1960. Optics of thin films. North Holland Publishing Company, Amsterdam.

Table 1. A list of iridescent plants observed in Malaysia

GREEN PLANTS

TAXON	FAMILY	DISTRIBUTION	COMMENTS
Cyathodium foetidissimum Schffn.	Marchantiaceae (Hepacopsida)	S. E. Asia	Seen at mouth of dark cave, Batu Caves, this and other taxa that grow in very dark locations appear iridescent green.
Monophyllaea patens Ridl.	Balsaminaceae	Limited to a few limestone outcrops in W. Malaysia.	Seen inside sanctuary cave Batu Caves. The related *M. horsfieldii* Ridl. is iridescent, but to a lesser extent.
Begonia sinuata Wall.	Begoniaceae	S. E. Asia	Common on shady and damp rocks in forest. Other *Begonia* species also have iridescent green leaves, but to a lesser extent.
		BLUE PLANTS	
Selaginella willdenowii (Desv.) Bak.	Selaginellaceae	Extremely common in S. E. Asia and also in temperate greenhouses.	Perhaps the most frequently encountered blue-leaved plant. Other species may also be iridescent, AS *S. atroviridis* (Wall.) Spring.
Lindsaea scandens Hk. var. *terrestris* Holtt.	Dennstaedtiaceae (Lindsaeoideae)	Low forest and mountain valleys throughout the peninsula.	Other species of *Lindsaea* (perhaps L. *ucida* Bl.) may have a blue metallic sheen to the leaves.
Athyrium crenatoserratum (Bl.) Milde	Dennstaedtiaceae (Athyrioideae)	Common in low and mid-elevation forest in S. E. Asia.	The older leaves have a metallic blue sheen. Also reported for *Athyrium cordifolium* (Bl.) Copel.
Polystichopsis hanifii (Holtt.) Holtt.	(Dryopteridoideae) Dennstaedtiaceae	In high mountain valleys, West Malaysia.	
Phyllagathis rotundifolia Bl.	Melastomataceae	Common in low elevation forest in South East Asia.	After *S. willdenowii* the most common blue iridescent plant.
Begonia pavonina Ridl.	Begoniaceae	Rare in West Malaysia. Deep forest from low to high elevation.	Striking for the bluish-purplish coloured leaves, this turning to gold as the leaf is turned.
Mapania sp.	Cyperaceae	South East Asia.	Common iridescent blue plants in Sarawak.
Didymochlaena *Truncatula* (Sw.) J. Sm.	Dennstaedtiaceae (Dryopteridoideae)	West Malaysia, and perhaps elsewhere in South east Asia.	at medium elevations in mountain areas.

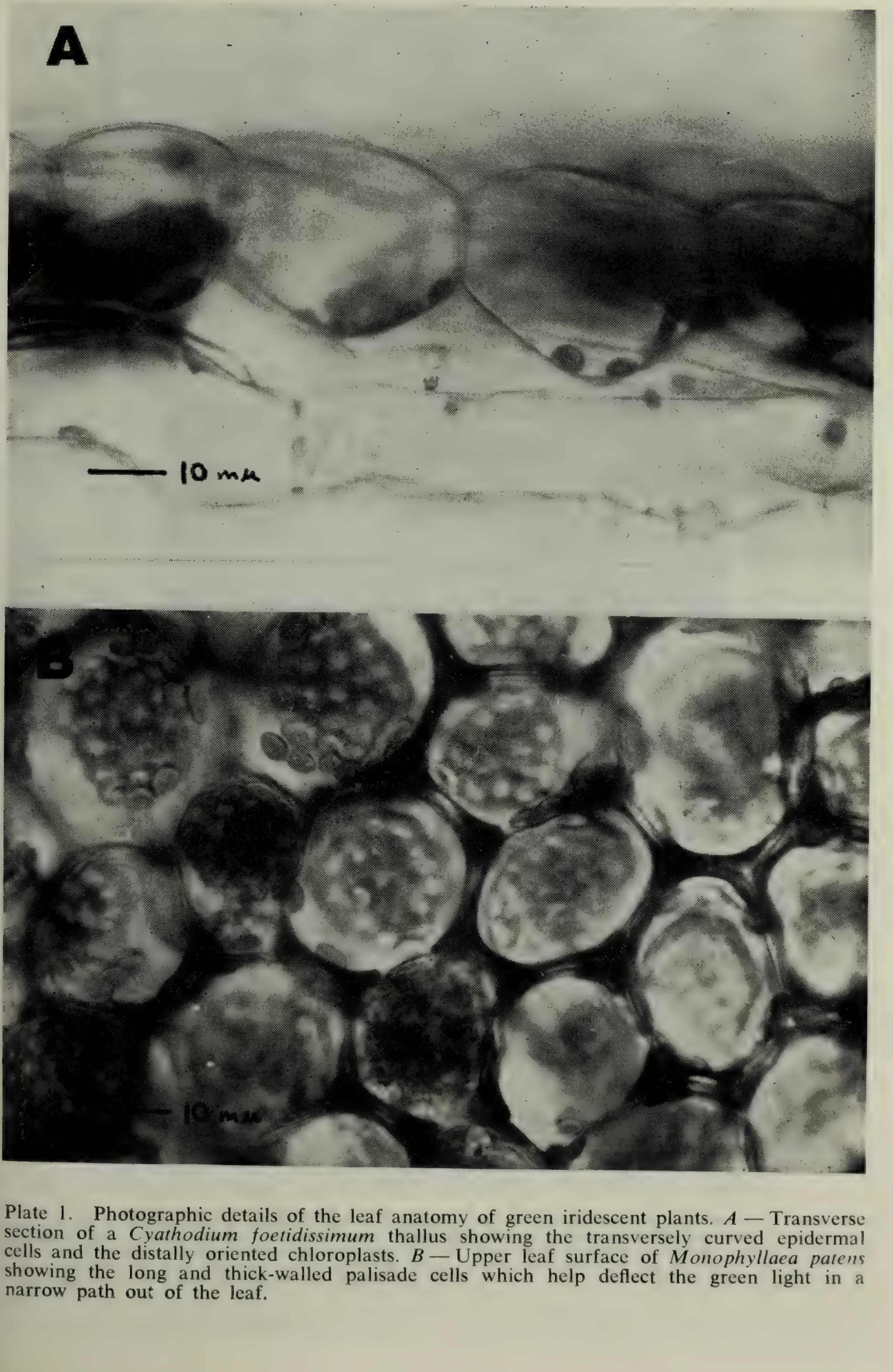

Plate 1. Photographic details of the leaf anatomy of green iridescent plants. *A* — Transverse section of a *Cyathodium foetidissimum* thallus showing the transversely curved epidermal cells and the distally oriented chloroplasts. *B* — Upper leaf surface of *Monophyllaea patens* showing the long and thick-walled palisade cells which help deflect the green light in a narrow path out of the leaf.

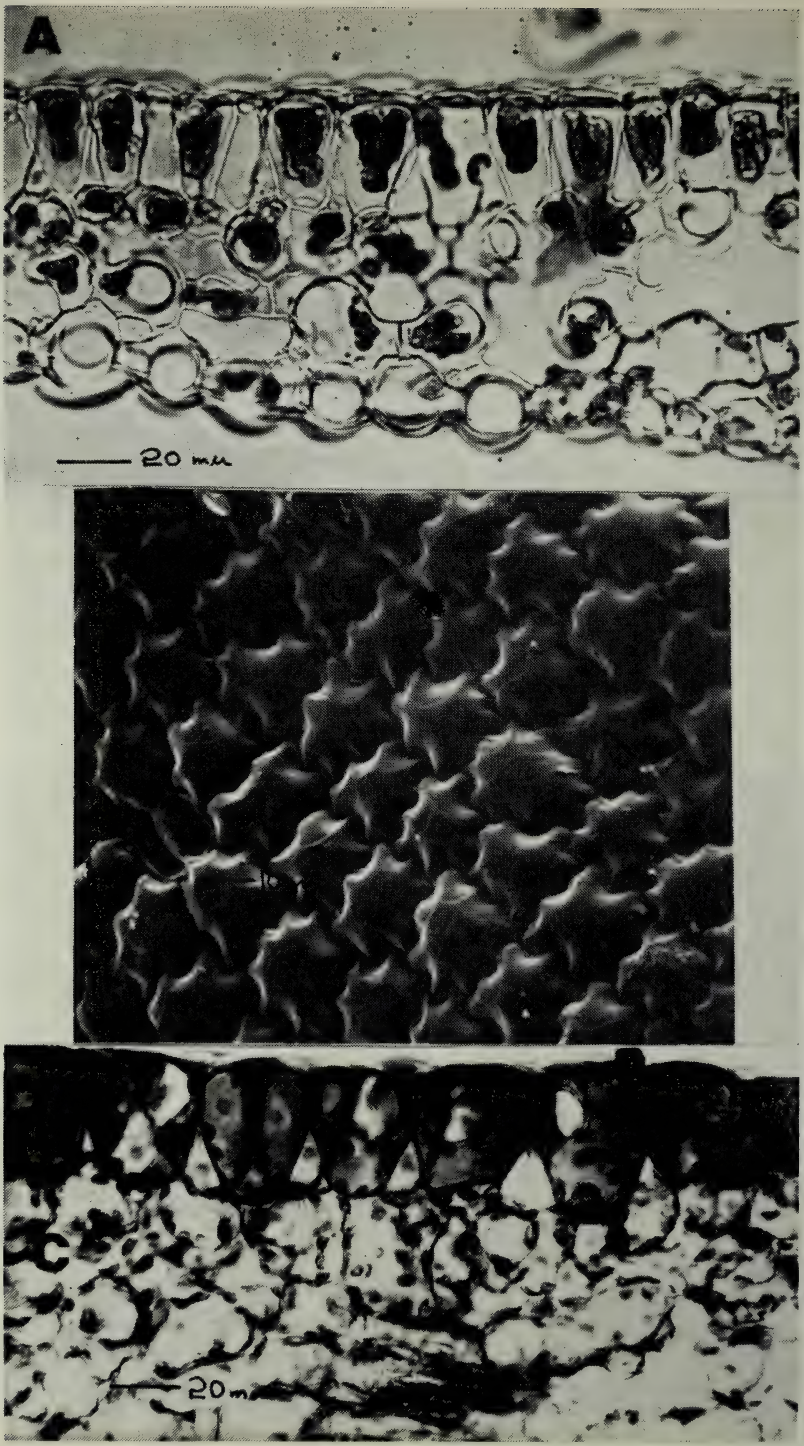

Plate 2. Photographic details of the leaf anatomy of blue iridescent plants. *A* — Transverse section of *Selaginella willdenowii* leaf. Note the peculiar shape of the epidermal cells and the large single chloroplasts. *B* — Scanning electron micrograph of the surface of the *S. willdenowii* leaf; the convex curvature of the epidermal cells is easily seen. *C* — Transverse section of leaf of *Athyrium crenatoserratum.* Note the convexly curving epidermal cells. The two transverse-section photographs are courtesy of Encik Jayamohan Krishnan; SEM micrograph was supplied by Encik Ho Kok Wai.

The Ferns of Gunong Ulu Kali

by

A. G. Piggott *

Summary

The various habitats on the peak of Ulu Kali and in the surrounding area, the Genting Highlands, are described. Some one hundred species and varieties of ferns found between 5,000 feet and the summit are listed.

Gunong Ulu Kali is the southernmost high mountain peak in the Main Range of Malaya, and is only 20 miles NNE of Kuala Lumpur. The environment and vegetation of the mountain and surrounding area, the Genting Highlands, have been described briefly by Burgess (1969). Before the Hotel and Casino Complex was opened in 1971, this part of the Main Range could only be reached by walking and climbing through the jungle. Now, at Genting Simpah, a road branches off the main Kuala Lumpur/Kuantan trunk road and winds its way to the top. At about 5,000 feet, with one mile still to go, the character of the vegetation changes. The trees are smaller, gnarled and mossy. There are fewer climbers, abundant lower down, and fewer tree ferns. Higher still, the vegetation changes again and becomes the dwarf and scrub forest of the Cloud Zone. The trees here are stunted; there is little or no grass and epiphytes are abundant.

Though few people venture beyond the Complex, the road continues. Your vehicle can take you within yards of the summit of Gunong Ulu Kali (5,814 feet), and along the whole length of the ridge to Bukit Genting Chin Chin. The slopes are steep or precipitous, and treacherous. On a clear morning the views from the ridge are spectacular: neighbouring mountain peaks covered with jungle, the City of Kuala Lumpur, the tin mines, and, in the far distance, the sea. It is cool, refreshing and still. If cloud descends, it becomes chilly, visibility is limited to a few yards and strong winds may blow.

The area studied includes Gunong Ulu Kali and the associated ridge, and also some lower slopes towards the two pumps supplying the Complex with water. The ferns listed were all found between the summit and about 5,000 feet. It was not possible to record every species in all places, but the list does give an indication of their frequency and distribution. For convenience, the area was divided into a number of locations, each the centre of forays into the various habitats nearby.

Ferns of Malaya (Holttum 1966) was used as an aid to identification, but since the publication of the second edition, the author has reappraised the family Thelypteridaceae (1971) in which sense the generic names are used here. Specimens were deposited at the Herbarium of the Royal Botanic Gardens at Kew, and an incomplete set also at the Botanic Gardens, Singapore.

DESCRIPTION OF LOCATIONS

A is situated at the end of the road along the ridge, 1.75 miles from the car park. The Radar Station occupies the small peak just beyond. There are still remnants of scrub forest nearby, and lower down the steep slopes is montane ericaceous forest, with conifers and Pandanus. Earthmoving has been carried out on a large scale, leaving cleared areas and fresh earth banks. Drainage is channelled

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* 21, Jalan Dato Klana, Seremban, Malaysia.

into a steep mossy valley on the eastern side, and this was where *Habenaria angustata,* a terrestrial orchid, was found. It was growing in mossy peat and on rotting tree-trunks.

B is 0.15 mile along the road, back towards the Hotel Complex. The ground drops away sharply to the east. On the opposite side of the road are wet mossy hollows with *Pandanus klossii,* and above them dwarf forest. The trees support an abundant flora of mosses and lichens, and epiphytic ferns and orchids. In September and October some trees were almost covered with pinkish purple orchid flowers. A large crested lizard was first seen here.

Equisetum debile was growing in sand near the roadside drain at 0.25 mile. Over a period of one and a half years it developed from a small tuft to a large straggling mass.

C is 0.3 mile along, at the point where the road changes from one side of the ridge to the other. Strong winds blow through the gap. Large granite boulders form pinnacles with tree-roots growing over the weathering surfaces. Above the road is dwarf mossy forest; at road level there are cleared areas and earth banks; and then the ground drops away on either side. *Pholidota parviflora* grew here, and *Coelogyne* sp. with fleshy red scapes and drooping racemes of flowers on long pedicels. Further on, the road has been blasted out of the rock of the ridge and there is a precipitous drop of about 1,000 feet on the western side. Here, an almost horizontal vein — apparently decomposing felspar — has been exposed. The road then crosses back to the east side of the ridge.

D, at 0.4 mile, is rather open. In the valley are larger trees, raising their crowns to the level of the ridge, and tall tree ferns. Earth banks border the road. Fragrant *Coelogyne longibracteata* and *Dendrochilum simile* were common and flowered towards the end of the year.

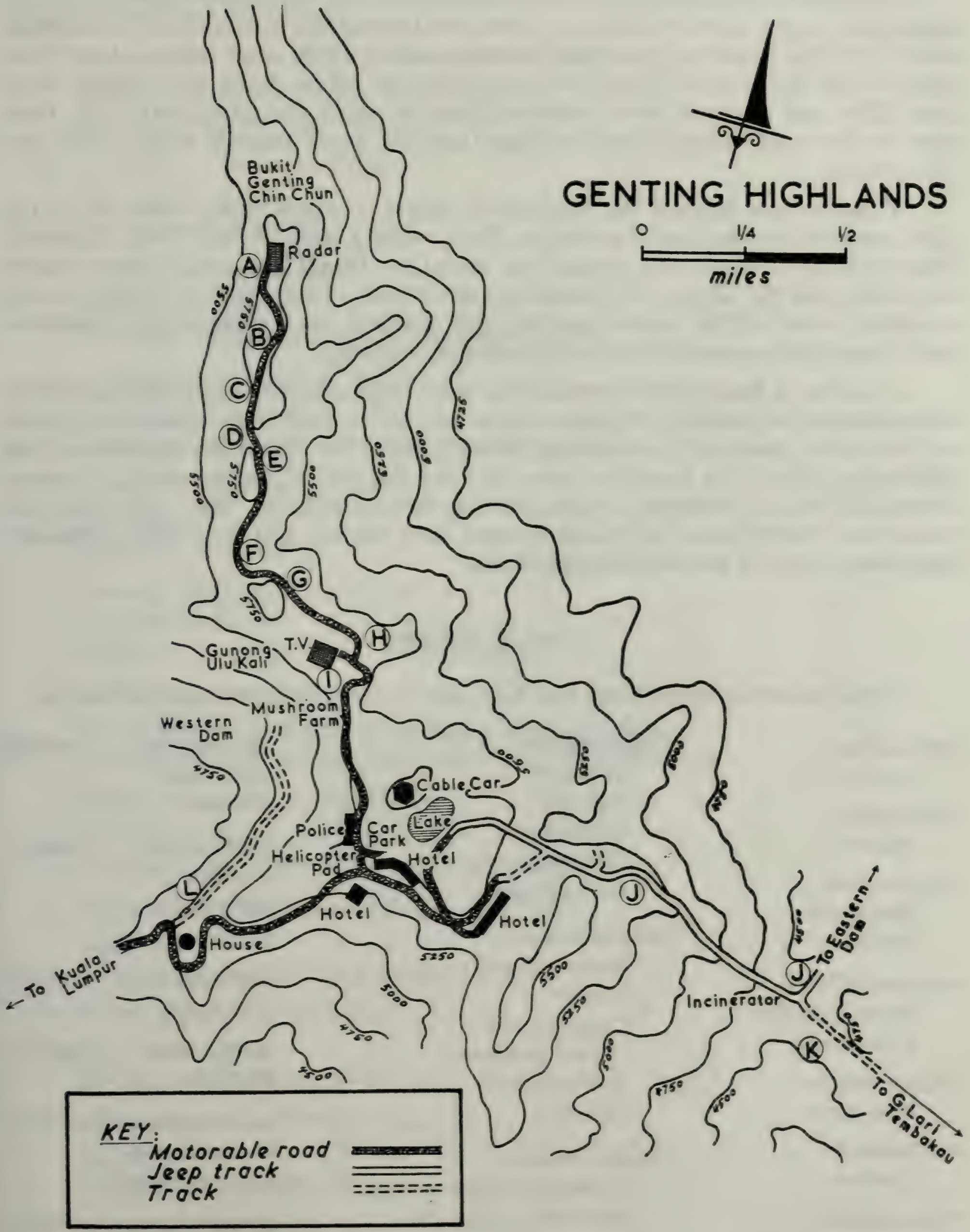
E is at 0.5 mile, with large trees in the valley below. The stunted forest above contains a high proportion of conifers which have the habit of dropping the ends of their branches. *Bulbophyllum angustifolium* was in flower in February. There are wet mossy hollows where epiphytic ferns are abundant and the fruiting bodies of macroscopic fungi can be found.

F is very exposed at 0.8 mile, the road running almost along the crest of the ridge. There are fresh earth banks, patches of secondary growth, fallen trees, dwarf forest and the heads of small steep valleys. An established path goes into the forest behind but care should be taken: it often becomes a running stream, and there are scorpions.

G, 0.95 mile, is somewhat sheltered. The trees are larger and some have fallen, making identification of epiphytes growing in the crown much easier. *Coelogyne longibracteata* was abundant and flowered late in the year. *Dendrobium cornutum* and *D. atrorubens* produced flowers in July. Wild bananas, ginger and a variety of creepers can be seen. Terrestrial ferns with large fronds grow on the edge of the clearing.

H is 1.1 miles along the ridge and there is a large clearing, an abandoned building site, to the east. Beyond this a path leads into scrub forest on a short northerly ridge. The stunted trees, which included *Dacrydium beccarii* and *Rhododendron orion,* are barely 6 feet tall and grow in thick peat and sphagnum root mat. An arborescent grass was growing near the end of this ridge. *Dischidia astephana* and some *Nepenthes* spp. were also here. In July many flowers of *Habernaria angustata* were found. Dwarf forest grows on the other side of the road and mossy hollows drain into streams which pass under the road.

I: Gunong Ulu Kali, 1.25 miles along the ridge and 0.5 mile from the Complex. The Television Station has been built on the summit, but just below and across the site of the construction workers' hut is an area of nearly undisturbed scrub forest.



The twisted trees are covered with mosses, lichens and epiphytes. From here the road winds downhill, with steep debris-covered slopes to the east. Further still the road has been cut into the side of the mountain and the natural environment has been much disturbed. Little remains of the natural vegetation: pioneer species are becoming established.

Locations *J, K* and *L* cover larger areas, down to an altitude of about 5,000 feet:

J is the land adjacent to the track which leads to the eastern dam and pump house, and begins north of the main hotel and beyond the boating lake. It descends some 1,000 feet, running round the mountain-sides. Deep road cuttings have been made in the steep slopes. The incinerator and main refuse dump are situated along here. This area is much more sheltered than the ridge and some very large trees grow in the main valleys. Near the dam there are small swamps which drain into the streams.

K begins just beyond the incinerator, where a rough track bears off to the right towards Gunong Lari Tembakau. For a while a pack of 'wild' dogs inhabited those parts of it where the ground has caved in. Dwarf and scrub forest clothes the peaks, but the slopes are shaded by taller trees. There are some large mossy boulders in one of the wetter patches, and amongst these *Cryptostylis arachnites* and *Ceratostylis ampullacea* were flowering in January.

L is along a track which turns off the main road, one mile down and just below the residence 'Sri Genting'. It more or less follows the 5,000 foot contour and leads to the western dam and pump-house, directly under the Television Station and the Mushroom Farm. The track has been cut into the side of the mountain. It passes through fairly tall sheltered forest, crossing several streams. Wet rock faces are found near the streams, in places covered with mosses and liverworts, including *Marchantia* sp., but few Hymenophyllaceae.

LIST OF GENERA

Ferns occurring on Gunong Ulu Kali, above 5,000 feet, arranged in families.

- Schizaeaceae
  - *Schizaea*
- Matoniaceae
  - *Matonia*
- Gleicheniaceae
  - *Gleichenia*
  - *Dicranopteris*
- Hymenophyllaceae
  - *Hymenophyllum*
  - *Trichomanes*
- Plagiogyriaceae
  - *Plagiogyria*
- Cyatheaceae
  - *Cyathea*
- Polypodiaceae
  - *Dipteris*
  - *Belvisia*
  - *Loxogramme*
  - *Microsorium*
  - *Crypsinus*
  - *Goniophlebium*
  - *Lecanopteris*
- Grammitidaceae
  - *Grammitis*
  - *Xiphopteris*
  - *Calymmodon*
  - *Ctenopteris*
  - *Scleroglossum*
- Thelypteridaceae
  - *Macrothelypteris*
  - *Chingia*
  - *Coryphopteris*
  - *Sphaerostephanos*
  - *Pneumatopteris*
  - *Christella*
- Dennstaedtiaceae
  - Dennstaedtioideae subfam.
    - *Microlepia*
    - *Hypolepis*
  - Lindsaeoideae subfam.
    - *Lindsaea*
    - *Sphenomeris*
  - Davallioideae subfam.
    - *Davallia*
  - Oleandroideae subfam.
    - *Nephrolepis*
    - *Oleandra*
  - Pteridioideae subfam.
    - *Pteridium*
    - *Histiopteris*
    - *Pteris*
  - Asplenioideae subfam.
    - *Asplenium*
  - Blechnoideae subfam.
    - *Blechnum*
  - Lomariopsidoideae subfam.
    - *Elaphoglossum*
    - *Teratophyllum*
  - Dryopteridoideae subfam.
    - *Acrophorus*
  - Athyrioideae subfam.
    - *Diplazium*
- Adiantaceae
  - *Pityrogramma*
  - *Vittaria*

LIST OF SPECIES AND VARIETIES

Ferns occurring on Gunong Ulu Kali, above 5,000 feet, arranged alphabetically, with locations and brief notes.

1. *Acrophorus blumei* Ching apud C. Chr. Plate 1.
   Locations: A, E, G, K, L.
   In shady hollows and valleys.
2. *Asplenium caudatum* Forst.
   Locations: J, K, L.
   On rocks by streams.
3. *Asplenium nidus* Linn.
   Locations: J, L.
   Epiphytic on larger trees in the deeper valleys.
4. *Asplenium scortechinii* Bedd.
   Location: J.
   Epiphytes on mossy trees near the dam.
5. *Asplenium unilaterale* Lam.
   Location: L.
   In rocky stream-bed.
6. *Belvisia revoluta* (Bl.) Copel.
   Locations: J, L.
   Epiphyte on mossy trees in wet hollows.
7. *Blechnum orientale* L.
   Locations: H, and between I and Hotel Complex.
   On earth banks and exposed rock faces, often stunted.
8. *Blechnum vestitum* (Bl.) Kuhn
   Locations: A, B, C, E, I, J, K.
   In dwarf forest with *Plagiogyria tuberculata.*
9. *Calymmodon cucullatus* (Nees & Bl.) Presl
   Location: J.
   Small epiphyte on mossy trees near dam.
10. *Chingia pseudoferox* Holtt.
    Locations: I, L.
    In the open by roadside drains.
11. *Christella arida* (Don) Holtt.
    Location: I.
    In open by roadside drain.
12. *Coryphopteris badia* (v.A.v.R.) Holtt.
    Location: G.
    First record for Malaya.
    In light shade in mossy hollows.
13. *Coryphopteris gymnopoda* (Bak.) Holtt.
    Locations: A, B, E, I, L.
    In light shade in dwarf forest.

14. *Coryphopteris gymnopoda* (Bak.) Holtt. var. *bintangensis* Holtt.
    Location: B.
    On forest edge.

15. *Crypsinus enervis* (Cav.) Copel.
    Locations: A, D, E, G, H, J, K.
    Epiphyte in moderately exposed places.

16. *Crypsinus laciniatus* (Presl) Holtt. Plate 2.
    Locations: B, E, G, H, J, K, L.
    Epiphyte in open places.

17. *Crypsinus wrayi* (Bak.) Copel.
    Locations: A-C, E, G-L.
    Small epiphyte on very mossy trees.

18. *Ctenopteris contigua* (Forst.) Holtt. Plate 2.
    Location: H.
    Epiphyte in mossy hollow.

19. *Ctenopteris fuscata* (Bl.) Kze
    Locations: E, J.
    Small epiphyte in dwarf forest.

20. *Ctenopteris khasyana* (Hk.) Holtt.
    Location: E.
    Epiphyte in mossy hollow.

21. *Ctenopteris mollicoma* (Nees & Bl.) Kze
    Locations: A, J.
    Epiphyte in exposed situations.

22. *Ctenopteris moultonii* (Copel.) C. Chr. & Tard.
    Location: J.
    Epiphyte in sheltered valley.

23. *Ctenopteris obliquata* Copel.
    Location: J.
    Epiphyte in sheltered valley.

24. *Ctenopteris tenuisecta* (Bl.) J. Sm. Plate 1.
    Locations: H, J, K.
    Larger epiphyte in deep valleys.

25. *Cyathea contaminans* (Wall. ex Hook.) Copel.
    Locations: E, G, I, J, K.
    Large tree fern, on edge of forest and in valleys.

26. *Cyathea hymenodes* Mett.
    Locations: F, G, H, J.
    Tree fern on edge of dwarf forest.

27. *Cyathea hymenodes* Mett. (variety). Plate 1.
    Location: H.
    Tree fern on edge of clearing. I consider this sufficiently different from the species in its much reduced pinnae on the base of the stipe, to call it a variety for the time being.
    Collections. 21.06.75: *1334* (SING), *1335*, & *1337* (K), *1338* (SING).

28. *Cyathea lurida* (Bl.) Copel.
Locations: B, C, E, F, G.
Tree fern in dwarf forest along ridge.

29. *Davallia trichomanoides* Bl.
Location: J.
Epiphyte in sheltered valley.

30. *Davallia trichomanoides* Bl. var. *lorrainii* (Hance) Holtt.
Location: L.
Epiphyte, in light shade.

31. *Dicranopteris curranii* Copel.
Locations: F, G, J, K.
On fairly exposed earth banks.

32. *Dicranopteris linearis* (Burm.) Underwood var. *linearis* Holtt.
Locations: B, H, I.
Colonising exposed clearings.

33. *Dicranopteris linearis* (Burm.) Underwood var. *montana* Holtt.
Locations: F, H, J.
On side of road cuttings.

34. *Dicranopteris pubigera* (Bl.) Nakai
Locations: G, I.
On roadside banks in exposed situations.

35. *Diplazium accedens* (Bl.) Milde
Location: L.
In small sheltered valley.

36. *Diplazium asperum* Bl.
Locations: E, G, H, J, L.
On edge of forest.

37. *Diplazium speciosum* Bl.
Locations: B, C, D.
In fairly exposed situations near end of ridge.

38. *Dipteris conjugata* Reinw.
Locations: G, H, I, J, K.
Colonising steep earth banks.

39. *Elaphoglossum* sp. Plate 2.
Locations: A, B, C, D, F, G, H, J, K.
Epiphyte in less exposed places.
A new species which will be published and probably as *E. robinsonii.*
Differs from *E. callifolium* and *E. malayense* in having pale brown, thin, flat, entire scales and very broadly pointed lamina. It matches exactly an incomplete specimen collected by H. C. Robinson in 1913 on nearby Gunong Mengkuang.
Collections. 12.10.74: *1093* (K); 9.11.74: *1095* (SING); 10.11.74: *1094* (K); 10.08.75: *1339* & *1340, 1344-1347, 1358* & *1359* (all K).

40. *Gleichenia hirta* Bl. var. *amoena* (v.A.v.R.) Holtt.
Locations: F, G, I.
In fairly exposed grassy clearings.

41. *Gleichenia longissima* Bl.
Locations: F, G, H, I, J.
Scrambling on edge of forest.

42. *Gleichenia microphylla* R. Br.
Location: I.
In scrub forest and grassy clearing.

43. *Gleichenia truncata* (Willd.) Spr. var. *plumaeformis* (Presl) Holtt.
Locations: B, G, I, L.
Scrambling on edge of forest.

44. *Gleichenia vulcanica* Bl.
Locations: F, G, H, I.
In and on edges of dwarf and scrub forest.

45. *Goniophlebium persicifolium* (Desv.) Presl
Locations: J, K, L.
Epiphyte in sheltered places.

46. *Goniophlebium prainii* (Bedd.) C. Chr.
Locations: E, G, L.
Epiphyte on larger trees in valleys.

47. *Grammitis hirtella* (Bl.) Tuyama
Locations: H, I, J.
Epiphyte in dwarf and scrub forest.

48. *Grammitis hirtella* (Bl.) Tuyama var. *major* Holtt.
Locations: A, H, I.
Epiphyte in very mossy dwarf forest.

49. *Grammitis reinwardtii* Bl.
Locations: A, B.
Epiphyte on mossy trees.

50. *Histiopteris incisa* (Thunb.) J. Sm.
Locations: D, I, J, K, L.
Scrambling, on edge of forest.

51. *Histiopteris stipulacea* (Hk.) Copel.
Location: K.
On edge of small clearing.

52. *Hypolepis punctata* (Thunb.) Mett.
Location: E.
Few patches of small fronds in sandy clearing.

53. *Hymenophyllum acanthoides* (v.d.B.) Rosenst.
Locations: A, E, G.
Abundant on some mossy tree-trunks.

54. *Hymenophyllum blandum* Racib.
Locations: B, H.
Small epiphyte in dwarf forest.

55. *Hymenophyllum exsertum* Wall. ex Hook.
Locations: A, B, C, H, I, K, L.
Epiphyte on mossy trees.

56. *Hymenophyllum javanicum* Spr.
Location: J.
Epiphyte in valley near dam.

57. *Hymenophyllum serrulatum* (Presl) C. Chr.
Locations: I, K, L.
Epiphyte in less-exposed forest.

58. *Lecanopteris carnosa* (Reinw.) Bl. Plate 1.
Locations: H, K, L.
Epiphyte in crowns of trees. Easily accessible in scrub forest of small ridge.

59. *Lindsaea malayensis* Holtt.
Locations: E, G, H, J, K.
In wet mossy rocky hollows, and sometimes on rotting fallen trees.

60. *Lindsaea oblanceolata* v.A.v.R.
Locations: H, K, L.
Climbing in wet hollows; *L. pectinata* of 'Ferns of Malaya'.

61. *Lindsaea rigida* J. Sm.
Location: I.
In sheltered parts of mossy forest, climbing.

62. *Loxogramme avenia* (Bl.) Presl
Location: J.
Epiphyte and on rocks in wet valley near dam.

63. *Macrothelypteris torresiana* (Gaud.) Ching
Locations: A, I.
In the open by roadside drains.

64. *Matonia pectinata* R. Br.
Location: I.
On the top of roadside bank, very exposed, near summit.

65. *Microsorium sarawakense* (Bak.) Holtt.
Location: L.
Epiphyte near dam.

66. *Nephrolepis davallioides* (Sw.) Kze
Locations: E, J.
Epiphyte on few large trees in deeper valleys.

67. *Nephrolepis tuberosa* (Bory) Presl
Locations: I, J.
Fronds small, in peat at edges of clearings.

68. *Oleandra pistillaris* (Sw.) C. Chr.
Locations: G, H, J, K, L.
Straggly shrub in open sheltered places. Plants of a different habit, creeping and producing fronds singly, found on the middle part of the ridge.

69. *Pityrogramma calomelanos* (L.) Link
Locations: B, E, I, J, K.
Usually a small plant, rapidly becoming established on earth banks and in clearings.

70. *Plagiogyria tuberculata* Copel.
Locations: A, B, C, E, F, J, K, L.
Abundant in wet dwarf forest, with *Blechnum vestitum.*

71. *Pneumatopteris ecallosa* (Holtt.) Holtt.
Location: G.
In shade on side of valley.

72. *Pteridium aquilinum* (L.) Kuhn var. *wightianum* (Ag.) Tryon
Locations: D H, I.
Colonising earth banks and small clearings, and rapidly becoming more common.

73. *Pteridium caudatum* (L.) Maxon var. *yarrabense* Domin
Location: H.
One patch on edge of clearing.

74. *Pteris longipinnula* Wall.
Location: L.
In shelter of forest.

75. *Pteris tripartita* Sw.
Location: I.
Single well-developed fertile plant on steep slope of debris.

76. *Pteris vittata* L.
Locations: B, E, I.
Common by side of road, but fronds often small.

77. *Schizaea malaccana* Bak.
Locations: H, I.
In moss on dwarf trees in sheltered hollows.

78. *Scleroglossum minus* (Fée) C. Chr.
Locations: A, B, G, H, I, J, L.
Epiphyte in mossy forest.

79. *Scleroglossum pusillum* (Bl.) v.A.v.R.
Location: H.
Epiphyte in scrub forest on small ridge.

80. *Sphaerostephanos polycarpus* (Bl.) Holtt.
Locations: A, B, I.
In exposed situations by roadside drains. Differs from lowland specimens in having a more hairy lower surface and lacking glands on the upper surface, but matches one collected on Taiping Hills by Day in the 1880s.

81. *Sphenomeris chinensis* (L.) Maxon var. *divaricata* (Chr.) Kramer
Locations: G, J, L.
On steep earth banks and cuttings.

82. *Teratophyllum aculeatum* (Bl.) Mett. var. *montanum* Holtt.
Location: L.
High-climbing, clothing trunks of tall trees in valleys; upper limit of species about 5,000 feet.

83. *Trichomanes meifolium* Bory
Locations: A, B, E, F, H, I.
Epiphyte in mossy dwarf forest.

84. *Trichomanes obscurum* Bl.
Locations: C, J.
In wet peaty hollows.

85. *Trichomanes pallidum* Bl.
Locations: G, H.
Epiphyte on shadier side of mossy trees; fronds almost white.

86. *Trichomanes palmatifidum* C. Muell.
Location: C.
Epiphyte in moss on dwarf trees. Probably more abundant but difficult to detect.

87. *Vittaria angustifolia* Bl.
Location: F.
Epiphyte in mossy forest.

88. *Vittaria elongata* Sw.
Location: L.
Epiphyte in shady forest.

89. *Vittaria elongata* Sw. var. *angustifolia* Holtt.
Location: L.
Epiphyte in forest.

90. *Xiphopteris hieronymusii* (C. Chr.) Holtt.
Locations: A, C, F, H, I, J, K.
Epiphyte in mossy forest.

91. *Xiphopteris sparsipilosa* (Holtt.) Holtt.
Locations: B, J.
Epiphyte in mossy forest.

List of Unidentifiable Numbers

92. *Asplenium* sp., possibly *A. pellucidum* Lam.
Location: J.
Epiphyte in small wet valley near dam.
Collection. 10.11.74: *1092* (K).

93. *Belvisia* sp.
Location: L.
Specimen from small valley near dam.
Collection. 10.11.74: *1171* (K).

94. *Ctenopteris* sp.
Location: A.
Small epiphyte on mossy tree.
Collection. 12.10.74: *1055* (K).

95. *Cyathea* sp., probably *C. obscura* (Scort.) Copel.
Location: J.
Small sterile plant growing near track.
Collection. 10.11.74: *1217* (K).

96. *Diplazium* sp., near *D. pallidum* Bl.
Location: J.
Fertile fronds from side of track.
Collection. 10.11.74: *1011* (K).

97. *Diplazium* sp.
Location: L.
Incomplete fertile frond from edge of forest.
Collection. 19.07.74: *1085* (K).

98. *Hymenophyllum* sp., possibly *H. polyanthos* Sw.
Location: E.
Epiphyte on tree in valley.
Collections. 12.10.74: *1146* & *1147* (K).

99. *Microlepia* sp.
Location: G.
Single plant with sterile fronds only, much more hairy than *M. puberula;* under observation but lost during road improvements.
Collections. 9.11.74: *1175* (K) & *1176* (SING).

100. *Trichomanes* sp., probably *T. maximum* Bl.
Locations: H, I.
Fertile fronds from wet mossy hollows.
Collections. 2.02.75; *1144* (K) & *1145* (SING).

101. *Trichomanes* sp.
Location: L.
Sterile frond from mossy forest.
Collection. 19.07.74; *1248* (K).

The list of fern species was compiled after numerous expeditions to Gunong Ulu Kali over a period of about four years. Records of previous plant collections of that place are few. Burkill (1927) indicates that Burn-Murdoch obtained specimens from the mountain in 1910, and that Robinson sent an expedition to nearby Gunong Mengkuang Lebah in 1913. Ridley (1922-25) mentions the conifer *Dacrydium elatum* growing at 2,000 feet on Gunong Ulu Kali, and the Singapore Herbarium has a record of one of his collections there in 1914. More recently Mrs. Allen (1963) collected ferns at Genting Simpah, a few miles away and at a much lower altitude. And in 1973 and 1975 the staff of the Herbarium, Singapore Botanic Gardens, collected some ferns but mainly flowering plants from the summit of Gunong Ulu Kali. Further visits could well produce records of more and new fern species.

During recent years development has transformed the mountain peak into a new hill resort. This has resulted in changes in the composition and distribution of the flora. In view of the proposed expansion and further development of the Genting Highlands it would be interesting to follow these changes due to those in the habitat.

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References

Allen, B. M. (1963). Ferns of the Quartz Ridges. *Mal. Nat. J.,* **17**: 19–32.

Burgess, P. F. (1969). Ecological factors in hill and mountain forests of the States of Malaya. *Mal. Nat.. J.,* **22**: 119–128.

Burkill, I. H. (1927). Botanical Collectors, Collections, and Collecting Places in the Malay Peninsular. *Gard. Bull. Sing.,* **4**: 113–203.

Holttum, R. E. (1966). Ferns of Malaya (Revised Flora of Malaya, Vol. II) 2 ed. Govt. Print. Office, Singapore.

——————— (1971). Studies in the Family Thelypteridaceae III. *Blumea,* **19**, 17–52.

Ridley, H. N. (1922-25). Flora of the Malay Peninsula, Vols. I–V. Reeve, London.

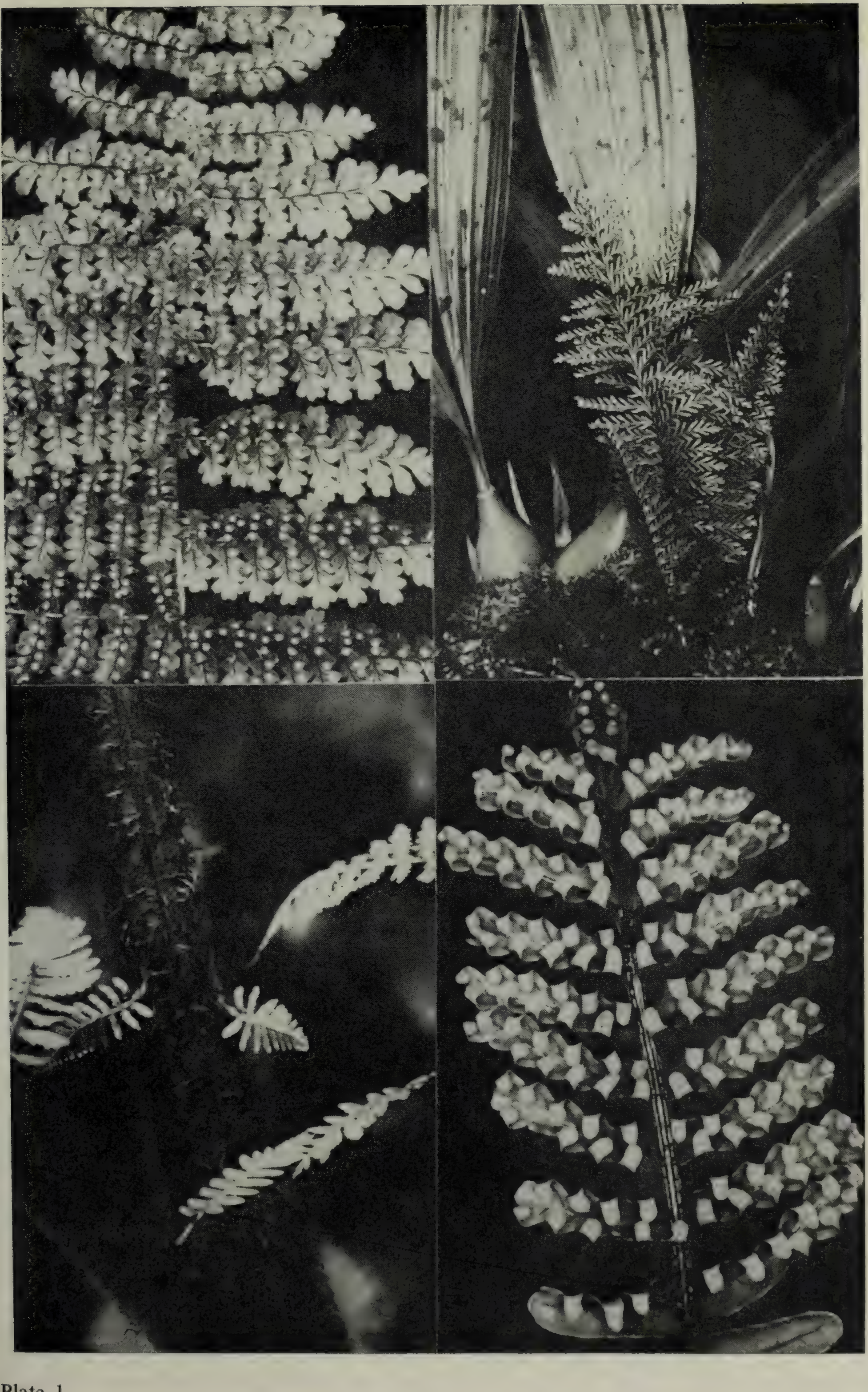

Plate 1.
Top left: *Acrophorus blumei*, part of fertile pinna, × 1.
Top right: *Ctenopteris tenuisecta* and orchid, × ½.
Bottom left: *Cyathea hymenodes*, variety with reduced pinnae, × 1.
Bottom right: *Lecanopteris carnosa*, apex of frond with soral flaps, × 1.

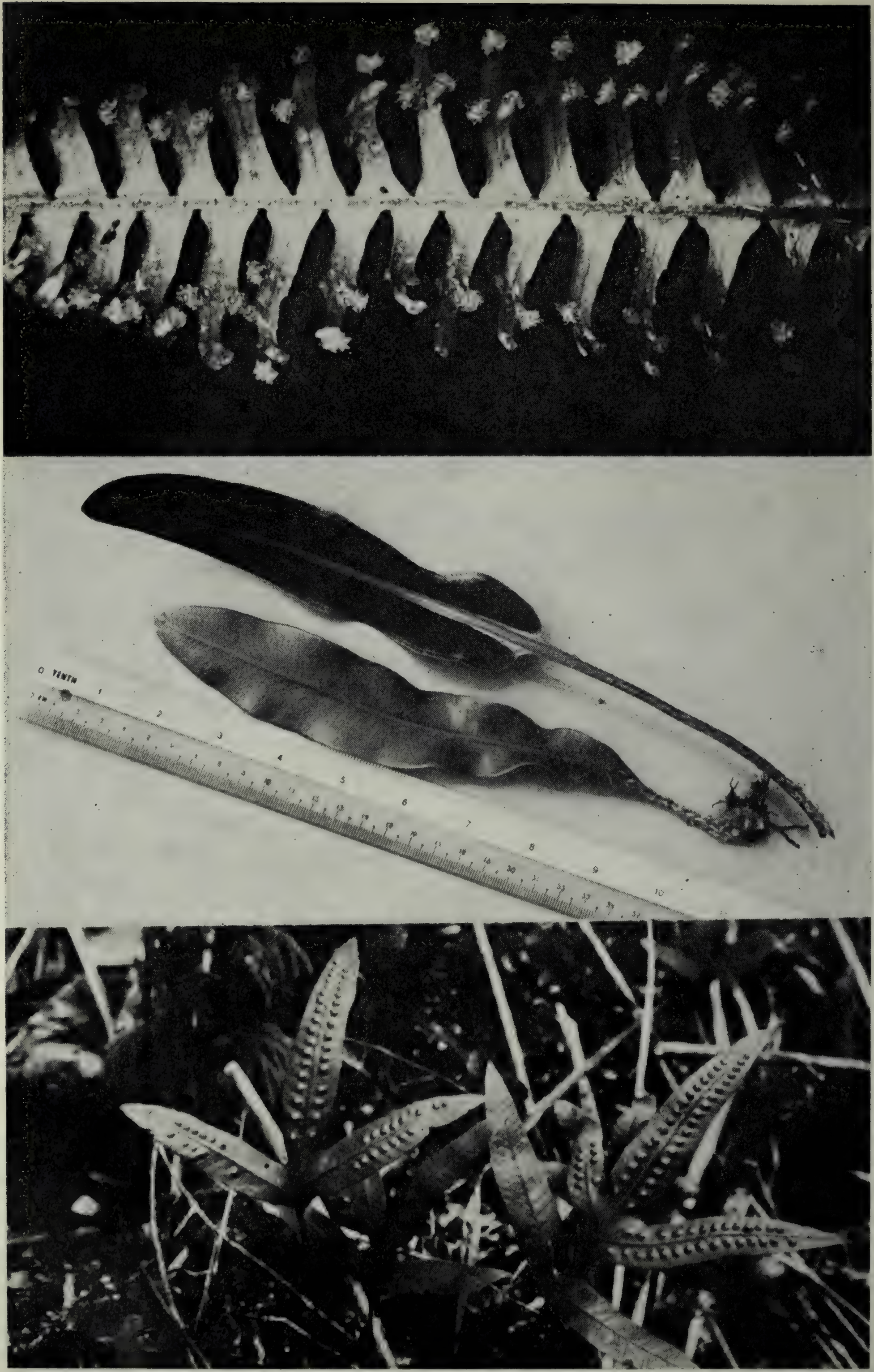

Plate 2.
Top: *Ctenopteris contigua*, part of fertile lamina, × 2.
Centre: *Elaphoglossum* sp., fertile (above) and sterile (below) fronds.
Bottom: *Crypsinus laciniatus*, fertile fronds, × ½.

Specific Concept in Humata pectinata (J. E. Smith) Desv.

by

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Introduction

The genus *Humata* Cav., of Davalliaceous affinity, is a typically tropical East Asian group of ferns, extending with a few outlying species to Madagascar in the West, Japan in the North and far into the Pacific to the East, but having its centre of distribution in Malesia. Thus, several species of *Humata* occur in Malaya-proper and the reader may be referred to the account of the genus in Holttum's well-known book on the ferns of Malaya (1954).

Holttum remarks on the difficulty of specific delimitation in the genus generally, caused by plasticity and variability, also to be observed, by the way, in other genera of the same relationship, like *Davallia, Scyphularia,* etc. In fact, Holttum suggests in the elaborate observations he makes under the specific descriptions that several species described from adjacent regions are doubtfully distinct from the Malayan Humatae recognized by him. But in the case of *Humata pectinata* (J. E. Smith) Desv., additional comment is limited to a short note on its ecology.

Still, a long history is attached to the name *Humata pectinata,* also as to how it should be interpreted and it may therefore be interesting to follow the vicissitudes of the specific concept that have been attached to this name.

Historical Account

It was perhaps ironical that J. E. Smith (1793), when first describing *Davallia pectinata,* based his diagnosis on two specimens, collected in localities that could hardly have been farther apart. He had received these plants from Banks and after the diagnosis Smith added:

> "Habitat in India Orientali, D. Hurloch 1786, eandem forte in Otaheite legit Nelson. H. Banks."

Alston (1933) commented on these types, still present in the Smith Herbarium now at the Linnean Society in London, in a publication that will be more fully discussed further on. It should be mentioned at this stage that Alston convincingly explained that Hurloch's plant came most probably from the Nicobar Islands, i.e. the most westerly limit of the distributional area of the *Humata pectinata* alliance, whereas the Nelson plant came from the most easterly (Otaheite = Tahiti).

The lamina of the two types are narrow-deltoid, the lowest segments being the largest. However, the basiscopic side of the lowest segments in the Hurloch-collection has only one prominent lobe, whereas the Nelson-collection has several, gradually passing distally into smaller crenations towards the segmental apex.

Gaudichaud (1827) described and illustrated *Nephrodium gaimardianum,* typified by a specimen now at Paris from Lawak (= Rawak) Island near Waigeu off West Irian, collected by his friend Gaimard. This must be considered an entirely independent description: no mention is made of J. E. Smith's publication and the likeness of *N. gaimardianum* to Smith's plant. The fern Gaudichaud illustrates is slightly narrower, lanceolate, and has one lobe on the lowest pair of segments.

A year later Wallich published his list (1828) and gave the name *Davallia parallela* to the Singapore collection No. 251. Wallich's names are "nomina nuda", but *D. parallela* was validated by Hooker, as shown hereunder.

Wallich's plant is hardly different from Gaudichaud's type of *Nephrodium gaimardianum,* with one small lobe on the lowest pair of segments.

Blume (1828) misconstrued *Davallia pectinata* J. E. Smith and gave that name to a species of *Prosaptia,* at the same time describing *Davallia intermarginalis* from Java, the type (at Leiden) being closely comparable to Gaudichaud's and Wallich's types. Blume's name was recognized as a synonym at an early stage in subsequent literature.

A beautiful plate of *Davallia pectinata* J. E. Smith was issued by Hooker & Greville (1831, pl. 139). The leaf is narrow-deltoid with many basiscopic lobes on the lowest pair of segments ("pinnae"). It was drawn from a specimen, collected by Menzies in Tahiti and resembles closely J. E. Smith's Nelson type of the same origin.

It is significant that Hooker at that time had no doubts that Menzies' plant is conspecific with *both* the syntypes of J. E. Smith, as clearly indicated in the elaborate text, accompanying the plate and in which Smith's type-localities are specially mentioned:

> "Hab. In insula Otaheite Menzies. In Malacca et in insulis Nicobar dictis. Smith."

Amongst the above basic descriptions Hooker (1846) made a critical choice in his monumental "Species Filicum". He retained two species, *Davallia pectinata* J. E. Smith and *Davallia parallela* "Wall". These taxa were, according to Hooker "undoubtedly nearly allied, but distinct", to be separated by the following characters:

> *a.* *D. parallela* has the shape of the frond less deltoid, also not so deeply divided and therefore never really pinnate, as in *D. pectinata.*
>
> *b.* Margins of segments (pinnae) are horizontally patent and entire, whereas in *D. pectinata* they are spreading and crenate.
>
> *c.* Lower margin of lowest pair of segments generally with one solitary lobe, rarely more; in *D. pectinata* pinnatifid with several lobes.
>
> *d.* Indusium opening to apex of segments; in *D. pectinata* opening obliquely to the (crenate) margin.

Apart from these two species, Hooker described *Davallia parallela* var. β, based on Cuming 61 from Luzon (BM, L), previously determined by J. Smith (1842) as *Humata pectinata* (J. E. Smith). It has no lobing of the lowest pair of segments, merely auricles.

As to the nomenclature adopted by Hooker: Wallich's name was deemed acceptable and thus "parallela" was given priority over Gaudichaud's epithet "gaimardiana" which is mentioned in synonymy. Blume's spurious conception of "Davallia pectinata" was not understood (Hooker had not seen Blume's types). "Java, Blume" is included in the enumeration of collectors and localities mentioned under *D. pectinata* and at the same time *Davallia intermarginalis* Blume is mentioned as a (doubtfully) separate species, the description from the Enumeratio being merely literally cited on the following page of the "Species Filicum".

That Hooker had his doubts on the origin of Smith's Hurloch type — and by inference on Blume's "Davallia pectinata" — is indicated by his remark under *D. pectinata*:

> "Sir Jas. Smith gives the East Indies as a locality, on the authority of Mr. Hurloch, but perhaps erroneously, for I have never seen it from the Continent of India, only from the Pacific".

This interesting note also clearly shows that Hooker still considered the syntypes of J. E. Smith to be conspecific; moreover, that an initial concept was developing in Hooker's thoughts as to a possible geographical separation of his two species.

At this stage a short review of the generic assignment of the taxa under discussion would be appropiate. Hooker had a very broad and mostly unnatural conception of the genus *Davallia*, as originally conceived by J. E. Smith. However, in the case of *D. parallela* and *D. pectinata*, being definitely Davalliaceous ferns, an inclusion in Davallia-proper could be defended, especially as Hooker lists these taxa as belonging to the subgenus *Humata* (Cav.). Still, in Hooker & Baur's (1842) "Genera Filicum", *Humata* Cav. is recognized as a proper genus, distinct from *Davallia* J. E. Smith, having an indusium that is free at the sides. As this subject is not falling within the strict scope of this article, it may suffice to say that in modern literature the genus *Humata* is universally recognized. One must add, however, that it is clearly and closely allied to *Davallia* s.str. and although only differing from *Davallia* virtually in one character, is an easily definable group and perhaps is best regarded as a "Genus of convenience", to speak with Copeland.

Continuing the historical review on the subject: in the Synopsis of Hooker & Baker (1867) the two species were maintained, but the differentiating characters were for the greater part eliminated. In fact, the only clearly definable feature left was the lobing of the lowest segments: pinnatifid "with lobes sometimes ½ inch long" in *Davallia pectinata*, whereas in *D. parallela* "the lowest pair (is) sometimes auricled". Gone are the differences in frond-form (described as ovate-lanceolate in both species); the orientation of the sori (oblique in both species); the pinnate or pinnatifid condition (being cut down nearly or quite to the rachis in both species). Hooker commented under *D. pectinata*: "Quite similar to the preceding [*D. parallela*] in size and texture".

D. intermarginalis Blume was no longer mentioned. "D. pectinata Blume non Smith" was included in the synonymy of *D. contigua* var. *D. blumei* Mett. [= *Prosaptia*] in the Appendix. *D. gaimardiana* (Gaud.) was mentioned in the synonymy of *D. parallela* as oldest name, but not (surprisingly) adopted.

The geographical details were given as: *D. parallela* in Malayan Peninsula and Polynesian Islands; *D. pectinata* in Tropical Polynesian Islands only.

Hooker's views had a deciding influence generally in the last century and in this particular case maybe up till now. To mention a few examples, Brackenridge (1854) recognized *Humata pectinata* "J. Smith" from Tahiti, *H. parallela* "(Wall)" from Samoa, enthusiastically referring to Hooker's (later discarded) differentiation in the "Species Filicum" regarding the orientation of the sori. Presl. (1849) conceived a new genus *Pachypleuria*, differing from *Humata* Cav. mainly in non-dimorphic fronds, and made the new combinations *Pachypleura parallela* (Hooker) Presl and *P. pectinata* (J. E. Smith) Presl, the former being even assigned by Fée (1852) as sole species to yet another genus, *Pteroneuron*, differing by (pseudo) dorsal sori, but neither gave any new ideas on the specific delimitation of the species in question.

The situation seemed to have been consolidated by Christensen (1906) in his Index, where he recognized *Humata gaimardiana* (Gaud.) J. Smith (Syn. *Davallia* *parallela* [Wall.] Hooker) and *Humata pectinata* (J. E. Smith) Desv., the former occurring from Burma through Malesia to Polynesia, the latter in Polynesia only.

There is in this period, however, one notable exception. It was Luerssen (1871) who, in his description of the ferns in the Fiji and Samoan Islands, strongly commented on the weak differentiation given by Hooker between *Davallia parallela* and *D. pectinata*:

> "Alle angegebenen, sogar von Hooker und Baker noch festgehaltenen Merkmale, welche die Davallia parallela Wall von Davallia pectinata trennen sollen, taugen nicht".

which is to say that, according to Luerssen, even the few means of differentiation, maintained in Hooker & Baker's Synopsis, most emphatically do not hold good. His elaborate comments clearly point to the many transitions, even on the same plant, that exist in the characters, supposed to serve as differential, all being variable within the traditional specific delimitation of both taxa.

Luerssen gave a full and complete list of the synonymy, in which *Davallia pectinata* J. E. Smith is included, but nevertheless adopted the later name *Davallia gaimardianum* (Gaud) "Presl", for which reason is obscure. Presl's combination is even illegitimate according to present rulings, having been published in the Tentamen (1836) with a query-mark and as a synonym in the Epimelia (1849).

Apart from Diels (1899) nobody ever took notice of Luerssen's view and it remained a lone cry in the — taxonomic — wilderness, one might say.

Christensen's influence on and significance for modern taxonomic fern-studies has been reemphasized quite recently by Holttum (1975). It is therefore no wonder that the former's specific concept on the subject taxa in the Index (1906) and the modified version in the Third Supplement (1933) — further discussed below — can be retraced in all modern regional floras in the Far East, to mention only: Van Alderwerelt's (1908) Malayan Ferns, Backer & Posthumus' (1939) Varenflora van Java, Tardieu & Christensen's (1939) Flore Générale de l'Indochine Vol 7, Holttum's (1954) Ferns of Malaya and Copeland's (1958) Fern Flora of the Philippines; and as far as the Pacific is concerned: Copeland's (1929 and 1932) treatises on the ferns of Fiji- and Society Islands, Christensen's (1943) revision of the Pteridophyta of Samoa and Brownlie's (1969) Pteridophyta of New Caledonia.

In the Third Supplement Christensen also recognized and confirmed several new species that had been described in the meantime as belonging to the same alliance.

Van Alderwerelt van Rosenburgh (1920) proposed *Humata lanuginosa* from Sumatra, syntypes Lörzing 4567, 4764 and Bünnemeyer 3881 (BO, L). In his description there is no character that is in any way new to the taxa discussed, apart from the profuse scaliness and the presence of hairs on the lower surface of the lamina.

There is another point in Van Alderwerelt's publication that deserves special comment. His types are all from Central Sumatra near Toba Lake, from 1100-1800 m, from where several other collections have been made, also from Mt. Dempo and Sibayak at higher altitudes. This is unusual, as elsewhere, also in Sumatra, collections are from the coastal plain or foothills and also often from the sea-shore.

The duplicate of Bünnemeyer's type-specimen, apparently sent to Leiden somewhat later, has the epithet "lanuginosa" deleted and "gaimardiana" written instead by Van Alderwerelt himself. This tends to show that the author did not believe long in his new creation; as several lamina of the syntypes show multiple lobing and going by the criteria that Van Alderwerelt had used in his Malayan Ferns, a rectification in *Humata pectinata* would have been more justified.

Copeland was more prolific. In his work on the Ferns of the Society Islands (1932) he remarks (p. 63):

> "Apparently in this group of [*Humata pectinata*] each island has developed a peculiar strain which might be construed as a distinct species".

but (fortunately) describes and illustrates only two, viz. *Humata huahinensis,* type Grant 5295 from Huahine and *H. melanophlebia,* type Grant 5144 from Tahaa (not seen). This self-imposed restriction is explained on p. 12 where, as on the other islands like Moorea and Bora Bora, "the characteristic representatives are less fixed in their pecularities and are accordingly left without distinctive names".

Humata huahinensis is described by Copeland as being very near to *H. pectinata,* but having a black stipe and deviating towards *H. gaimardiana* by being pinnatifid and position of sori, also the closely placed segments.

As to *Humata melanophlebia,* Copeland comments that it is like *H. huahinensis,* but pinnate with more remote pinnae (or segments more distally) which are clearly lobed, mainly basiscopically, the segments becoming inciso-serrate. Copeland (on page 63) mentions Grant's collection 5144 [= type of *H. melanophlebia*] again under *H. huahinensis.* Be that as it may, the proposed elevation to "species" of these Pacific representatives does not thereby become more convincing.

In 1940 Copeland described and illustrated another species, *Humata tenuivenia,* type Brass 14082 from New Guinea:

> "Humata pectinatae affinis, venis tenuibus inconspicuis, soris perlatis curvis, indusiis brevibus destincta".

The (iso)types (L and BO) and the photograph show these specimens to be robust plants from a shady wet habitat ("low epiphyte in coastal swamp-forest"). Copeland specially comments on the curved sori which can face the margin and apex or, in extreme cases, is curved so far that it faces at an angle to the costa too.

A few years earlier Copeland had been the instigator of yet another name. He had requested Alston to have a new look at J. E. Smith's types of *Davallia pectinata.* As a result, Alston (1933, l.c.) lectotypified *Davallia pectinata* J. E. Smith on the Hurloch specimen, dispersing Hooker's previous doubts as to the origin by showing that it came most probably from the Nicobar Islands and in any case from Western regions, not from the Pacific. Arguing further, Alston came to the conclusion that the name *Humata gaimardiana* (Gaud.) J. Smith (of Christensen's Index with a predominantly Western distribution) must in fact be replaced by *Humata pectinata* (J. E. Smith) Desv. and that the other syntype of J. E. Smith (Hooker's and Christensen's *Humata pectinata* with a Pacific distribution) had no name. Alston thus reversed the ideas hitherto current on geographical distribution, but maintained the traditional separation of two specific entities.

The new name Alston introduced was *Humata banksii* and the typification is based on the Tahiti collection No. 1769 (BM) by Banks, "Nelson's specimens being poor, both in the herbaria Smith and Banks". Alston's description emphasizes "profundae pinnatis" and "inferioribus margine inferiore pinnatifidis", otherwise does not give any further characters of differentiation from his *H. pectinata.* Actually Alston followed the description as included by Hooker & Baker in the Synopsis for (their) *Davallia pectinata.* Completely absent are comments on notably geographical distribution, or a comparison with e.g. Copeland's previously described species (1932) of which *H. huahinensis* is practically identical with Banks' plant. It is, as if Alston was wary to incriminate himself further in sorting out the antecedents of his new proposal.

Nevertheless, Alston's views, whether stated or only implied, were immediately followed by Christensen (1933) in the third Supplement of the Index and consequently in all the more local Flora's mentioned previously: Western plants now indiscriminately being called *Humata pectinata* (J. E. Smith) Desv., Eastern (Polynesian) plants referred to *Humata banksii* Alston.

But, Copeland did not agree. His comment on the Humatae in the "Oleandrid Ferns of New Guinea" (1940) may be appropriately quoted in full at the end of this historical survey:

> "This is the largest and most difficult genus of the group. Typically epiphytes, the individuals are subject to wide variations in exposure, and some of them are very responsive to these differences. Independent of the environment, some species seem to be notably variable ... Smith combined a Malayan and a Tahitian plant in describing Davallia (Humata) pectinata. H. parallela (Wall) Brack. and H. gaimardiana (Gaud.) J. Sm. were subsequently described in the same group. With many specimens from the Society Islands, it seemed to me that each island had its own, more or less distinct form, none of these like the comparatively uniform Malayan plant. It occurred to me that the Malayan plant might be the real H. pectinata, so I invited comparison of types by Mr. Alston. The result was his finding the Tahiti specimens [*sic*!] to be of two species, H. pectinata and H. banksii. It is my conclusion, not his that the Malayan plant must be H. parallela, for I have no Malayan specimen duplicated by any from Tahiti.
>
> Some characters which usually serve as specifically diagnostic, serve so badly in Humata. Size varies greatly as a matter of plasticity (response to environment). So with size does the dissection of the frond; and so probably do texture and laxness. Paleae are likely to be deciduous. And dimorphism is subject to some reversion.
>
> In the light of the foregoing discussion it will be understood that considerable work on this genus leaves me ill-satisfied. The presentation here given is the best I can make with the present material".

One could have full sympathy with this lament, were it not that in the ensuing key, size, dissection of frond, degree of scaliness and dimorphism figure prominently as differentiating characters. Of the 21 species, Copeland distinguishes in New Guinea alone, not less than six are described as new, of which one, *Humata tenuivenia* falls within the affinity of the taxa under review, as discussed above.

Copeland's confused rejection of Alston's interpretation of J. E. Smith's types was, for that matter, corrected later (1958) in the Fern Flora of the Philippines, where he uses the name *Humata pectinata* (J. E. Smith) Desv. for Philippine specimens, mentioning *Davallia parallela* "Wall" as a synonym.

Observations

When looking back on the features that have been used to distinguish between the taxa, as discussed heretofore, a hard core of only two characteristics remain, viz. the lobing of lowest pair of segments and the pinnatifid against the pinnate condition.

As to the last feature, the wing alongside the rachis is always distally broader than below and is, even in the most deeply incised leaves, never entirely absent. One cannot talk therefore of a real pinnate condition, it is always pseudo-pinnate and this variable point of distinction is in reality non-existent.

As to the (basiscopic) lobing of the lowest pair(s) of segments, transitions can be found on the same rhizome sometimes, from non- one-, two- to multi-lobed. A clinal pattern can be observed, whereby the multilobed basal segments become less frequent from East to West (nearly absent in Malaya and the Philippines), whereas the non-lobed or auricled/one lobed segments decrease from West to East, to being virtually absent in the Eastern Pacific.

The same pattern of gradual transitions can be found in the length of the lowest segments, being either longer, equal to, or shorter than the next pair, this making the overall leaf-shape either narrow deltoid, lanceolate/linear or narrow-ovoid. The sinuses vary in width from nearly equal to the width of the segments to mere slits, variable even on the same leaf or plant.

The above observations make differences in leaf-morphology unfit for the proper distinction of species and the recognition of *Humata banksii* Alston (and *Humata huahinensis* Copel.) seems to be based on weak ground.

Humata melanophlebia Copel. is an extreme case, where the lobing is also conspicuous on the next lower pair(s) of segments and more or less extended to the acroscopic side of the segments as well.

Differences in scaliness have hardly been used in proposing separate taxa, the variability in caducity and density having been generally understood. Van Alderwerelt's "hairs", described in *Humata lanuginosa,* are nothing but the highly dissected, hyaline squamules generally found — but not so obvious — on the underside of the lamina.

Actually, often the scales are not, or not well described, a glabrous or subglabrous condition prevailing in mature leaves. But young leaves (and stipes) are always scaly and the reader may be referred to Appendix I, where a full description of the scales can be found.

The venation is always ± flattened, conspicuous below, ± parallel with none or 1-2 forkings, 3 forkings only occurring in very large leaves, as in *Humata tenuivenia* Copel. The ancillary veinlet round the (terminal) sorus, basis for Fée's genus *Pteroneuron* can also be absent, or the veinlet is forked far below the sorus, thus becoming just a part of the normally forked venation, Transitions can be found even on the same segments.

The position and orientation of the sorus is also inconstant. It is always intramarginal and the indusium can be semi-circular to crescent-shaped, in extreme cases becoming reniform (*Humata tenuivenia* Copel.). Distally the sorus mostly faces the apex of the segment, lower down (obliquely) the margin.

Conclusion

The above review was made in the framework of a general study of the genus *Humata* Cav. — and other davallioid genera — the results of which will eventually be published in the Flora Malesiana. As such, Van Steenis' forceful, but lucid essay on "Specific Delimitation" is here considered an excellent guide to extricate oneself from further confusion. In itself the present study is an illustration of practically all the pitfalls, so convincingly summed up by Van Steenis, that can beset taxonomy and although his work is mostly based on vast experience in phanerogamic taxonomy, it is certainly also fully applicable to ferns.

Therefore, the author cannot but come to one conclusion, viz. that all the taxa under discussion can best be regarded as one polymorphic species with a wide distribution, for which the name *Humata pectinata* (J. E. Smith) Desv. should be used. Luerssen's views of nearly a hundred years ago are thus herewith fully confirmed.

Delimitation from allied species like *Humata repens* (Linn. f.) Diels, *H. vestita* (Bl.) Moore and *H. heterophylla* (J. E. Smith) Desv. gives no difficulty and shall not be further elaborated on in this context.

Recognition of infra-specific taxa is omitted; the variable, transitional (and clinal) nature of the characteristics, mentioned hitherto make them unsuitable for the delimitation of recognisable subspecies or varieties.

The geographic distribution of *Humata pectinata* as here construed is a clear-cut case of dependency on certain climatological circumstances. The area covers practically exactly and totally the zone of small seasonal variations in temperature (up to 35° F = 20° C) in the Eastern Tropics and Pacific, with the exception of that part of the zone which is liable to an appreciable monsoon. This explains the striking absence of the species from (East) Java, South-Sulawesi, Lesser Sunda Isles and Southern Moluccas in an otherwise continuous distribution throughout Malesia and Polynesia up to Tahiti. New Caledonia in the South and Taiwan in the North, in both of which islands the species is rare, are only just outside the zone as above referred to. Climatological maps covering the region can be found in Goode (1947).

A special note should be devoted to the occurrence of the species in Java. Although Blume's type of *Davallia intermarginalis* came ostensibly from Western Java, no further collections — apart from an old Junghuhn specimen at BO — have been made in that area for nearly 150 years. Nevertheless, potentially West Java (as against the eastern part of that island) could harbour our species, having only a weak monsoon. Could it have become extinct there by the vast destruction of lowland forest of that island?

The high-altitude collections in Central Sumatra have already been commented upon. This could be a special ecotype, but from New Guinea specimens from medium elevations (1100 m) are also known.

It could be argued that research of a karyological nature, especially cytogenetical, could produce better substantiated and more refined results than is possible by limiting the study to only herbarium material. Whilst this limitation is recognised it is regretted that such an approach is precluded by the unavailablity of live material. Whether it would really help in tackling the problem remains to be demonstrated. The mere thought of the difficulties involved in obtaining live plants from the whole distributional area and the time-consuming organization in rigging up a hybridization programme suggests that the above reserve if not illusory would, in practice be hard to tackle in a satisfactory way.

Finally this relatively uncomplicated, but nevertheless perforce lengthy account on how the species *Humata pectinata* has to be construed can be equally repeated for other taxa of the genus. As the publication of such detailed discussions would lead too far and be a tedious repetition, this study may serve as an example as to how the specific concept in the forthcoming treaties of the whole group will be maintained. That a considerable reduction in names will result — as already indicated by Holttum (1954) — is certain.

Acknowledgments

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Bibliographical References

v. Alderwerelt v. Rosenburgh, C. R. W. K. (1909) Malayan Ferns: 284–291.
——— . (1920) Bull. Jard. Bot. Bzg. 3/2: 155.
Alston, A. H. G. (1933) Phil. Journ. Sc. 50/2: 175–176, t. 1 fig. 1.
Backer, C. A. and Posthumus, 0. (1939) Varenflora Java: 96.
Blume, C. L. (1828) En. Pl. Javae, Fil.: 229, 230.
Brackenridge, W. D. in Wilkes, C. (1854) U.S. Expl. Exp. 16: 229.
Brownlie, G. (1969) Fl. Nouv. Cal. 3: 149.
Christensen, C. (1906) Index Fil.: 353, 354.
——— . (1934) Suppl. 3 (1917–1933): 112.
——— . (1943) Pter. Samoa, Bish. Mus. Bull. 177: 37.
Copeland, E. B. (1929) Ferns Fiji, Bish. Mus. Bull. 59: 89.
——— . (1932) Pter. Soc. Isl., Bish. Mus. Bull. 93: 11–12, 62–63, t. 12.
——— . (1940) Phil. Journ. Sc. 73/3: 350, t. 3.
——— . (1953) Fern. Fl. Phil.: 178.
Diels, L. (1899) Nat. Pfl. 1/4: 209.
Fée, A. L. A. (1852) Gen. Fil.: 320, 321, t. 25B fig. 1.
Gaudichaud-Beaupré, C. (1827) Freyc. Voy. Bot.: 335, t. 12 fig. 1.
Good, R. (1947), Geography Fl. Plants: t. 21, t. 24.
Holttum, R. E. (1954) Ferns. Mal.: 364–371.
——— . (1975) Taxon 24/4: 499–500.
Hooker, W. J. (1846) Spec. Fil.: 153, 154, t. 42A.
Hooker, W. J. & Baker, J. G. (1868) Syn. Fil.: 89.
Hooker, W. J. & Bauer, F. (1842) Gen. Fil.: t. 114A.
Hooker, W. J. & Greville, R. K. (1831) Ic. Fil.: t. 139.
Luerssen, C. (1871) Fil. Graeff., Mitt. Gesamtg. Bot. 1: 206–207.
Presl, C. B. (1836) Tent. Pt.: 79, 128.
——— . (1849) Epim. Bot.: 98.
Smith, J. (1841) Journ. Bot. 3: 416.
——— . (1842) London Journ. Bot. 1: 425.
Smith, J. E. (1793) Mém. Ac. Tprin 5: 415.
v. Steenis, C. G. G. J. (1957) Fl. Males. ser. 1, 5/3: CLXVII-CCXXXIV.
Tardieu-Blot, M. L. & Christensen, C. (1939) Fl. Gén. Indo-Chine 7/2: 109.
Wallich, N. (1828) List: No. 251.

APPENDIX I

NOMENCLATURE

Humata pectinata (J. E. Smith) Desv. (1827). Prodr.: 323. — *Davallia pectinata* J. E. Smith (1793) Mém. Ac. Turin 5: 415; *Trichomanes* Poir. in Lam (1808) Encycl. 8: 78; *Pachypleuria* Presl. (1849) Epim.: 98 — Type: Hurloch/Soc. Unit. Frat. s.n. from Ind. Or. (probably Nicobar Isl.) as lectotypified by Alston (1933) Phil. Journ. Sc. 50: 175, t. 1 fig. 1.

Nephrodium gaimardianum Gaud. (1827) Freyc. Voy. Bat.: 335, t. 12 fig. 1; *Nephrolepis* Presl. (1836) Tent.: 79; *Humata* J. Smith (1842) London Journ. Bot. 1: 425; *Davallia* [Presl. (1836) Tent.: 128 (comb. ill.)] Kuhn (1869) Zool. Bot. Ges. Wien: 580 — Type: Gaudichaud (Gaimard) s.n. from P. Lawak = Rawak/Waigeu/W. Irian.

Davallia parallela [Wallich (1828) List No. 251 (nomen nudum)] Hooker (1846) Sp. Fil.: 153, t. 42a; *Pachypleuria* Presl. (1849) Epim.: 98; *Pteroneuron* Fée (1852) Gen. Fil.: 320, t. 25b; *Humata* Brack. in Wilkes (1854) U.S. Expl. Exp. 16 Bot.: 229; *Oleandra* Keys. (1873) Pol. Cyath. Herb. Bung.: 41 — Type: Wallich 251 Singapore.

Davallia parallela var. β Hook. (1846) Sp. Fil.: 153 — Type: Cuming 61 Luzon.

Davallia intermarginalis Blume (1828) Enum.; 230; *Pachypleuria* Presl. (1849) Epim.: 98; *Humata* Moore (1861) Index: 296 — Type: Blume s.n. Java.

Humata lanuginosa v.A.v.R. (1920) Bull. Jard. Bot. Bzg. 3/2: 155 — Syntypes; Lörzing 4567, 4764, B. Baroe/Sumatra; Bünnemeyer 3881 G. Malintang/Sumatra.

Humata huahinensis Copel. (1932) Bish. Mus. Bull. 93: 11. t. 12b — Type: Grant 5295 Huahine/Soc. Isl.

Humata melanophlebia Copel. (1932) Bish. Mus. Bull. 93: 11, t. 12a — Type: Grant 5144 Tahaa/Soc. Isl.

Humata banksii Alston (1933) Phil. Journ. Sc. 50: 176 — Type: Banks 1769 Tahiti/Soc. Isl.

Humata tenuivenia Copel. (1940) Phil. Journ. Sc. 73: 350, t. 3 — Type: Brass 14082 Idenburg R./W. Irian.

DESCRIPTION

Rhizome upto several metres long-creeping, slender (1½–2½ mm), blackish with white-chalky patches, dictyostelic and dorsiventral, vascular tissue much dissected with two main bundles; bearing articulated fronds, on short phyllopodia, 2–5 cm or more apart; thickly set with appressed. imbricated scales, 4 to 5 mm long, ± 1 mm wide at the oblong peltate base, from there tapering to the acute apex, castaneous, the thin margin often hyaline/whitish, when young bearing marginal crinkly hairs which are mostly soon deciduous, the edge becoming entire at an early stage.

Stipe thin (1 mm ϕ) but firm, as long as, or somewhat shorter than the lamina, green to reddish brown when living, brown to blackish when dried, sulcate; vascular tissue with mostly three bundless, becoming fused upwards; loosely set with caducous scales and often entirely glabrous with age; scales like those of rhizome but not so appressed and more rounded, becoming smaller, paler, the edge more dissected.

Lamina firm, coriaceous, (5) 7–18 cm long, 4–6 (8) cm wide, narrowly deltoid, lanceolate/linear to narrowly ovate, dark green above, paler below, pinnatifid/pectinate with truncate/cordate base and short coadunate apex; segments many (12–30) which are sessile and confluent by a narrow wing along the rachis; wing occasionally inconspicuous between the lowest pairs of segments (the lamina then becoming pseudo-pinnate) but always widening upwards; sinuses deep and narrow, to about as wide as the pinnae but usually much narrower, becoming distally shallower towards the crenate to entire apex; rachis prominent, green to brown/blackish, sulcate except at the apex; scales loosely covering the young unfolding leaves, equal to those on the stipe, however, especially on the lamina becoming even more hyaline and dissolute, variously deciduous but mostly leaving a few traces on lower surface of rachis and costa, as well as on the margins of the often (sub) glabrous lamina.

Segments to 6 (8) mm wide, straight and horizontally patent or a little curved upwards, the apex bluntly acute to rounded; edge in barren leaves rarely quite entire, commonly shallowly crenate/sinuate at apex only, less often the incisions becoming more pronounced and continuing to bottom of sinus; in the very slightly and inconspicuously contracted fertile leaves incisions more prominent; the lowest pair of segments variable, either somewhat shorter or equal (ovate-lanceolate form), or if more developed, becoming longer than the next pair of segments (narrow-deltoid form), the basiscopic edge being either entire, auricled, often prominently, or two/multi lobed, the lobes grading to the crenated apex, the lowest segments then becoming unilaterally pinnatifid; venation, apart from the prominent costa, distinct on lower surface only, the veins coarse, brown and parallel, not or 1, 2, (3) times forked, both upper and lower basal primary veins springing from very base of costa or in larger fronds the lower directly from the rachis.

Sori terminal on the swollen acroscopic (when forked) vein-ending, forming an intramarginal, often crowded row; away from the apex often with an accessory posterior veinlet running round the sorus to just within the leaf-edge; indusium brown, ± 1 mm wide, finely striated, firm and permanent, semi-circular or crescent-shaped to reniform, the lower straight to convex side attached in the middle for ± half its length, otherwise the indusium free, opening to the apex or (especially lower down) obliquely to the leaf-edge; sporangia with 12–14 indurated cells; spores monolite, verrucate-rugulate, 20 x 13 μ with crenulated margin.

Geographical Distribution

From Southern Burma (Mergui), Lower Thailand, South Viet Nam, and Taiwan, throughout Malesia with the exception of those regions with an appreciable monsoon (Middle and Eastern Java, Lesser Sunda Islands, South-Sulawesi and South Moluccas), extending further into Tropical Polynesia to Society Islands in the East and New Caledonia in the South.

Ecology

Epiphyte, high and low, on trees; or terrestrial on boles and rocks, in often exposed habitats near seashore and in light forest, steep banks, even padangs on bare sand, but also known from swamp-forest in shade. Can apparently stand a lot of exposure, the leaves curling up in dry periods [Holttum (1954)]. From sea-level to 800 m, going up to 2000 m in Sumatra and to medium altitudes in New Guinea.

APPENDIX II

ILLUSTRATIONS

Various facies of *Humata pectinata* (J. E. Smith) Desv.

1. Sinclair, S. F. 40582 (1955) North side of Cape Rochado-Malacca-Malaya.
   "Rocky wooded seashore. Creeping rhizome on sea cliffs. Fruiting. Fronds curled up with the drought. Flattened by immersing in water".
   Two leaves from same rhizome.
2. Lörzing 15533 (1929), East Mt. Sibayak-Sumatra-Indonesia, 1300–1440 m.
   "Primary forest, epiphytic, and, in lighter places, on prostrate trunks and rocks. Not rare".
   Two fronds from same rhizome.
3. Lütjeharms 4674 (1936), Enggano off West Sumatra-Indonesia.
   "Epiphytisch op klapperstammen. Strand bij Kiojoh".
   Small leaves on rhizome.
4. Van Niel 3383 (1964), Tutong-Brunei-North Borneo.
   "Under clumps of trees in an open vegetation (sand)".
   Two leaves on same (branched) rhizome.
5. Cuming 61 (1836), Luzon-Philippines.
   No further details — Type *Davallia parallela* var. β Hooker.
   One leaf from isotype at L.
6. Brass 14082 (1939), Bernhard Camp-Idenburg River-W. Irian-Indonesia.
   "Low epiphyte in flooded rain forest of rive-plain at 50 m." — Type ***Humata tenuivenia*** Copel.
   One leaf from isotype at L.
7. Van Balgooy 1983 (1971), W. slope Pahia-Bora^2-Society Islands, 300 m.
   "Epiphyte, rootstock creeping".
   One large, one small leaf from same collection.


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Curcuma zedoaria

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My previous notes on the nomenclature of *Curcuma zedoaria* (Notes Roy. Bot. Gard. Edinburgh, 31: 226. 1972) were inaccurate. At that time I pointed out, correctly, that "*Amomum zedoaria* Berg.", which is always cited as the basionym of *Curcuma zedoaria*, has no existence as a binomial. I then said that the first valid publication of the name *Amomum zedoaria* was by Plenck in 1789, by which time the plant had already been named *A. latifolium* by Lamarck (1783). Where I, and others, have erred till now is in failing to notice that *Amomum zedoaria* was validly published in the German version of Houttuyn's *Natuurlijke Historie* by Christmann & Panzer (1779). Details of this work and its relation to Houttuyn's original publication are given by Merrill (in Journ. Arn. Arb. 19: 291. 1938). Briefly, the important point for our present purpose is that the work by Christmann & Panzer is not a literal German translation from Houttuyn: it incorporates both changes and new matter. Merrill listed all the new names he observed, but unfortunately *Amomum zedoaria* in the German version escaped him, and, not having the original work at hand, this helped to lull me into a sense of security. Although the work as a whole may be attributed to Christmann & Panzer, Merrill showed that new names appearing in volumes 1-7 should be attributed solely to Christmann.

Christmann cites a number of authors under *Amomum zedoaria*: Bergius, Rheede, Rumphius, Petiver and others. It is the description by Rheede under the name Kua which gives the most detailed and reliable account of this plant: this was cited by Bergius at the head of his references and formed the basis of Lamarck's *Amomum latifolium* and it is Rheede's illustration of it that was redrawn for Plenck's plate. There is every reason for taking this reference as the "lectotype" of the name *Amomum zedoaria* Christm., and this I accordingly propose.

Amomum zedoaria was published by Christmann in 1779 and it thus provides the earliest valid post-Linnaean epithet for a *Curcuma*. Its transfer to that genus may still be attributed to Roscoe, for Roscoe cites Willdenow and Willdenow gives the reference "Houtt. Linn. Syst. 5, p. 12" which proves to refer to the German edition of Christmann & Panzer. It may be noted that in Houttuyn's original Dutch edition (Handl. Pl. Kruidk. 7: 10. 1777) zedoary is referred to *Amomum zerumbeth*, which is *Zingiber zerumbet* (L.) Roscoe.

As the basis for the name *Curcuma zedoaria* is Rheede's description and plate it has seemed not without interest to supply a translation and reproduction.

Kua

Plate VII

Kua, in Brahmi *Acua*, is the special and common name for all those plants that ought to be referred to species of ginger; they are eight in number. *Kua, Tsjana Kua, Mallan Kua, Manga Kua, Mangella Kua, Intsyi Kua, Katou-Intsyi Kua.* The first species likes all soils, especially the sandy ones in which it grows spontaneously and spreads. The rhizome runs out horizontally from a single centre, white, thick, tuberous, with slender fibrous rootlets here and there, firm, run through with many whitish threads [i.e. vascular bundles], with glabrous skin; it is divided along its length into tuberous segments about two fingers thick and a span [c. 19 *cm*] long, branched, and filled with a clear juice. The taste is sharp, pinching the tongue, irritant, aromatic. The scent is strong and pleasant as if many aromas were mixed together. The leaves arise from the ends of the rhizome, up to a cubit [c. 46 *cm*] long and two spans [c. 38 *cm*] wide in the middle; acuminate at the tip, narrowed at the base, with a prominent midrib; this sends out many lateral veins, running transversely forward, equally spaced; they disappear at the extreme edge where they embrace the margin of the leaf with finer veinlets; the inner part of the leaf is somewhat folded and reflexed, marked with grooves. The colour on the inner part is dark, on the outer paler. For the rest the leaves are glabrous, shining, clear. The stems are a foot and a half high, full of greenish pith, but no shoots are to be seen on them; however, from the rhizome a special flowering stem arises, covered by a number of long leafy scales very closely enfolding it; and these leaves are more than a digit long, broadened upwards and then again contracted to a small point, with the tips bent back from the scape; they are glabrous with slender longitudinal veinlets which, unless they be broken, are nearly invisible; the lower ones are green, the middle ones yellow, the upper red purple or light blue, the uppermost becoming almost white, pretty, sweet-smelling, and tasting like the root. The flowers are produced in the gaps between the scales [i.e. bracts], 2 or 3 at a time, bell-shaped, the lower part and inside whitish, thin, enclosed in a transparent membrane [i.e. calyx], 6-petalled [i.e. with 3 petals and 3 petaloid staminodes] the upper one pellucid, shaped like a helmet, erect; they are yellow and white, folded, and scarcely to be seen unless the whole flower is separated from the stem and in turn taken apart itself, when one is seen to be bent down to a fimbriate margin; in the middle the flower produces a thread [i.e. the style] provided with a spur like a dragon's head, and recalling a little winged bird with erect tail [this refers to the spurred anther between the lobes of which the upper part of the style is held]. The scent is pleasant, but when the flowers are broken from the pouch and bruised between the fingers they have a similar smell to the leaves, and a rather bitter flavour. The seed capsules are small and round, depressed, and contain grey seeds like those of *Tsjana Kua*, but they are rarely found. The rhizome is long persistent; the leaves die down and shoot forth again in July and August. The grated roots, washed several times, leave a flour much valued by the indigenous peoples who make a porrage from it. A potion of bruised root and fresh juice arrests all inflammation of the intestines, purges the kidneys, stops white flux, cures gonorrhea and purges the blood. The juice of the leaves is drunk by people with dropsy, it takes away the swelling of the abdomen, is a moderate laxative, and expels the viscid slime of the intestines.

[Footnote by Commelin.] *Kua*, according to the opinion of the illustrious Paul Hermann is the garden *Zerumbeth* of Garcia [da Orta], whose description like that of the Arabic authors is rather obscure; by the Singhalese it is called *Walinghura*, that is wild ginger, the Malabars call it *Kua*. The opinion of Hermann agrees very closely with that of our author.

The other plants mentioned by their local names, of which the spelling varies slightly in different parts of the work, are:—

Tsjana Kua — Costus speciosus (Koenig) Sm.
Mallan Kua — Kaempferia rotunda L.
Manga Kua — Boesenbergia rotunda (L.) Mansf.
Mangella Kua — Curcuma longa L.
Intsyi Kua — Zingiber officinale (L.) Rosc.
Katou-Intsyi Kua — Zingiber zerumbet (L.) Rosc.
Mala-Intsyi Kua — Alpinia allughas (Retz.) Rosc.

Pars 11 Tab. 7

Kúa Lat

കൂവ Mal

Kúa

कुवा bram

قحوا Arab

Rheede's description does not, of course, give the precise technical detail that we look for to-day; for that we turn to Holttum's account of the Zingiberaceae of the Malay Peninsula (this Bulletin, 13: 71. 1950). Rheede, however, supplies a remarkably vivid account of a plant whose whole structure was a novelty at that time. It has not seemed justifiable to reprint the original latin, but those interested in the development of botanical terminology may be interested to note that in it *calyx* refers to the cup or pouch formed by the bract, *filamentum* to the thread-like style, and *pollen* to the flour obtained from the root.

I have referred throughout to Rheede. Hendryk van Rheede tot Draakestein was appointed Governor of the Dutch possession in Malabar in 1667. He organized the bringing together of the materials that were sent back to Holland and published as the Hortus Malabaricus. Burkill (Chap. Hist. Bot. India, pp. 6–7, 1965) tells us that the drawings were made by an artist-missionary Matthaeus, that the accounts of the plants were rendered into Portuguese by an interpreter and thence into latin by the secretary of the local government Hermann van Doner. Then drawings and descriptions were assembled by Johannes Casearius and were sent to Holland for publication, where they were edited partly by A. Seyn but largely, after Seyn's death, by J. Commelin who was in charge of the Hortus Medicus at Amsterdam.

Curcuma zedoaria is a species that has been in cultivation for a very long time and its natural origin has never been precisely established. This is a particularly difficult problem as it very easily becomes naturalized. In fact it is on record that although *C. zedoaria* very rarely flowers under conditions of cultivation, it does so freely where it runs wild. It is now found in most parts of India and south-east Asia. Like other members of the genus it dies down completely after flowering and has a resting phase: which at least suggests that its origin was in the monsoon areas rather than in Malaya. If, as often stated, it originated in N. E. India, this would be a good focal point for its spread south into peninsular India, east to China and SE to Malaya.

Synonymy and useful references are detailed below; those appearing in square brackets are not nomenclaturally valid names.

Curcuma zedoaria (Christm.) Roscoe in Trans. Linn. Soc. 8: 354 (1807) et Monandr. Pl. Scitam. t. 109 (1825); Horan., Monogr. Scit. 23 (1862); Baker in Hook. f., Fl. Brit. Ind. 6: 210 (1890); Trimen, Handb. Fl. Ceylon, 4: 241 (1898); K. Schum., Pflanzenr. Zingiber. 110 (1904); Gagnepain in Lecomte, Fl. Gen. Ind. Chin. 6: 67 (1908); Merrill, Enum. Phil. Fl. Pl. 1: 243 (1924) et in Trans. Amer. Phil. Soc. N.S. 24 pt. 2: 119 (1938); Burkill, Dict. Econ. Prod. Mal. Pen. 714 (1935); Holttum in Gard. Bull. Singapore 13: 71, fig. 5 (1950); Wealth of India 2: 405 (1950); Backer & Bakh. f., Fl. Java, 3: 71, 72 (1968).

Syn: [*Kua* Rheede, Hort. Malab. 11: 13, t. 7 (1692)]

[*Zedoaria* Camellus, Herb. Stirp. Luzon, Syll. 23 No. 9 in Ray, Hist. Pl. 3 App. (1704).]

[*Zedoaria officinarum* Petiver, Gagophyl. Nat. dec. 3, 5, tab. 23 f. 1 (1704–6?).]

[*Zerumbed vel Tommon* [*primum*] Rumph., Herb. Amboin. 5: 169 excl. t. 68 (1747) — fide Valeton in Merrill, Interp. Herb. Amboin. 164 (1917).]

[*Amomum scapo nudo, spica laxa truncata* Bergius, Mat. Med. 4 (1778), ed. 2, 4 (1782).]

Amomum zedoaria Christm. in Christm. & Panzer, Linn. Pflanzensyst. 5: 12 (1779); Plenck, Ic. Pl. Med. 2: 12, t. 11 (1789); Willd., Sp. Pl. 1: 7 (1797).

Amomum latifolium Lam., Encycl. 1: 134 (1783). Type: *Kua* Rheede.

Curcuma pallida Lour., Fl. Coch. 9 (1790) et ed. Willd. 12 (1793). Type: "in agrestis in Cochinchina et Cantone Sinarum" (no specimen known).

Curcuma zerumbet Roxb. in Asiat. Research. 11: 332 (1810) et Pl. Coromand. 3, t. 201 (1819); Alston in Trimen, Handb. Fl. Ceylon Suppl. 281 (1931); Burtt & Smith in Notes R.B.G. Edin. 31: 203 (1972) sub *Curcuma* (*Erndlia subpersonata* Giseke); nom. illegit.

Curcuma speciosa Link, Enum. Pl. Hort. Berol. 1: 5 (1821); nom. illegit.

Studies in the Systematics of Filmy Ferns

II. A note on Meringium and the taxa allied to this

by

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Summary

The evaluated taxonomic features of *Meringium* and the 'genera' allied to this are revised from the standpoint of comparative morphology. The features observed in detail are denticulation, hairs, internal cell walls, and sorus. Based on the observation of these features, the systems given by Copeland and Morton are critically discussed by the author who proposes several amendments for their systems, such as: *Hymenophyllum* s.str. is distinguished from *Meringium* only by the soral construction and *Mecodium* by the hairs and sorus; *Hemicyatheon* is identical with *Meringium;* and *H. levingei* is better segregated from *Hymenophyllum* s.str.

The species belonging to *Hymenophyllum* s.l. were classified into 13 genera by Copeland (1938, 1947). Among them the 'genera' centering to *Meringium* are treated here to revise the system of the filmy ferns. According to the definition by Copeland, *Meringium* is the genus of some 60 species in the tropics and southern hemisphere, having a combination of such features as: 1) the segments and wings of axes denticulate at margin, 2) the involucre closed at the lower portion with bivalvate upper portion, 3) the receptacles growing indefinitely and extruded from the lips of involucre, 4) cell walls thicker and coarsely pitted. These characteristics are not completely represented by some species referred to *Meringium*. In this part of this series, several taxonomic characteristics of *Meringium* are revised, comparing with those of *Hymenophyllum* s.l., especially with the 'genera' allied to *Meringium*, e.g. *Amphipterum, Buesia, Hemicyatheon, Leptocionium, Myriodon,* and *Hymenophyllum* s.str. including *H. levingei.*

Morton (1968) placed *Meringium* in *Hymenophyllum* subgen. *Hymenophyllum* and classified it as a distinct section named *Ptychophyllum* arranged next to sect. *Hymenophyllum.* In this system, he evaluated the denticulate margin of the ultimate segments, or of the wings as well, and separated *Amphipterum* and *Leptocionium,* placing them in subgen. *Mecodium* and *Sphaerocionium,* respectively. Copeland took much value, on the contrary, to the structure of sorus.

In the following discussion all the species will be named under *Hymenophyllum* s.l., pending the nomenclatural discussion until the system of the filmy ferns will be revised as a whole. The names of subdivisions of the family will be adopted in accordance with Copeland's system, or in some cases with Morton's.

Continued from the *Fern Gazette* 11 (2 & 3): 124.

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General features of Meringium sensu Copeland

Before going further, the general features of *Meringium* will be summarized comparing with those found in the 'genera' allied to this, although some of them will be treated in detail in the next section.

Rhizome. As usual in the case of *Hymenophyllum* s.l., the rhizome is long creeping, irregularly branched, wiry, nearly the same in thickness as or a little thicker than stipes. The apex is variously hairy with usually caducous hairs, the older portion being glabrous or very sparsely hairy. Roots are rather irregular in arrangement and bear hairs on all the surfaces.

Fronds. The size of fronds is variable according to the species, or even within a species to some extent. The smallest is found in *H. lobbii* bearing fertile fronds less than 1 cm in length including stipes. On the contrary, the largest frond of *H. penangianum* at hand is nearly 35 cm in length. The fronds seem to elongate to some extent in humid mossy forest forming slender outlines. *H. armstrongii* is referred to *Meringium* and has only a few lobes, and *H. lobbii, H. blandum* and several others are pinnate in plan or at most with the pinnae a few times forked. The larger fronds are pinnate several times with simple or forked ultimate segments. The outline of the ultimate segments is long and slender, or comparatively short and broader downwards.

Stipes are terete or winged nearly to the base. The hairs are present or absent according to the species; the presence on stipes correlates with that on other axes. The rachis is similar to the stipe, winged throughout in many cases. The wings on rachis and stipes are similar to the ultimate segments, denticulate or entire, plane or crisped, glabrous, and (2–) 4–12 (–25) cells broad.

The ultimate segments which, as in the filmy ferns in general, consist of one cell layer except for the costae, are round to obtuse at apex, denticulate, or entire in some species, plane to distinctly crisped.

Hairs. The hairs on the lower surface of axes, if any, are the same as those on rhizome. The coloration of the hairs is pale brown in the apical part of fronds and rhizome but dark brown in the older portion. The hairs are setose, pointed at apex, consisting of two to seven cells, and 0.5–2 mm in length.

In *H. johorense, H. reductum,* and *H. armstrongii,* multicellular setae are found at margin of segments, and in *Amphipterum* the multicellular hairs are at margin of accessory wing. Except in these cases, no hairs are found on the laminar portion of the fronds in *Meringium* and its allies.

Cell walls. The internal cell walls are thick and coarsely pitted in many species but not so thick and slightly waved in the others. This feature is evaluated by Copeland to distinguish *Meringium* from *Hymenophyllum* s.str.

Sorus. The involucre is obconic at base with distinctly bivalvate lips. The size of involucre is rather variable and the lips are entire or denticulate. In most cases, it has been observed that the accessories on the involucre are like wings or bundles of hairs. The receptacles are clavate, grow indefinitely and extrude from the lips of involucre.

Character phylogeny of four evaluated features

Among the diagnostic features for defining *Meringium* and the 'genera' allied to this, four important characteristics will be treated here to revise the system of the species in question. They are denticulation, cell walls, hairs, and sorus. The evolutionary trends within each of these features will be discussed to elucidate the phylogenetic importance of them.

1. DENTICULATION

The dentation of lobes is usually correlated with the veins for the megaphyllous leaves, though that of the filmy ferns in question is like that found in the lobes of the bryophytes without any actual relation to the veins. The marginal growth of the ultimate segments and wings as well is unequal, resulting in the irregular margin or the occurrence of denticulation, although the arrangement of it is regular in most cases (plate I). The denticulation here under consideration is, therefore, morphologically not homologous to that of vascular plants in general, though it will be described here under the term denticulation.

The denticulation occurs in various forms in the species of *Meringium*. The wings of rachis and costae are entire or denticulate, and the denticulate segments and wings are either plane or crisped. The lips of involucre are toothed in many species and entire in the others. The occurrence of denticulation is also various according to the species. In *H. edentulum* the denticulation is rather rare, while *H. meyenianum* and allied species have regularly denticulate margin of segments, and the segments and wings of *H. denticulatum* are copiously denticulate and crisped to some extent. The last tendency proceeds comprehensively in *H. acanthoides*.

The denticulate margin of ultimate segments is one of the key characters of *Meringium*, sharing it with *Hymenophyllum* s.str. Among the species of *Meringium* regarded by Copeland, however, there are several which have ultimate segments with entire margin: they are *H. macroglossum, H. pachydermicum, H. penangianum, H. pollenianum, H. pulchrum,* and *H. ricciaefolium*. Except for this characteristic feature of the entire margin of ultimate segments, they are close to the species of *Meringium*, or to *H. meyenianum*, in having the same morphology in hairs, cell walls, and sorus.

Contrary to this case, a few species referred to *Mecodium* by Copeland are included by Morton in sect. *Ptychophyllum*, an equivalent of *Meringium* in the system of the latter: they are *H. reinwardtii, H. samoense, H. taiwanense,* and *H. thuidium*. In the diagnostic features other than the denticulate segments, these four species are different from *H. meyenianum* as noted by Copeland, and by Tagawa (1940) for the third species. The margin of ultimate segments is copiously crisped for these species, and the denticulation seems to be more irregular (Fig. 2). The arrangement of laminar cells at margin of segments is irregular in *H. fimbriatum*, appearing somewhat denticulate, though the denticulation is different from that in *Meringium* species (Fig. 3). I prefer to exclude these species on the basis of their morphology in sorus, hairs, and cell walls in addition to the irregular denticulation at margin of segments, and would place them in *Mecodium* close to *M. javanicum*.

Accessory wings and *Amphipterum*

There are four species belonging to *Amphipterum* which is distinct in having accessory wings not in the plane of the lamina. Copeland (1938) distinguished *Amphipterum* generically from *Meringium*, although he (1937) had correctly suggested that 'I would not consider it expedient to distinguish it generically or otherwise if the wings on the veins were the only distinction'. I would follow Copeland to consider that *H. fuscum* and three other species are close to each other but are different from *Meringium* in combination of various features, admitting that the definition can be given solely upon the accessory wings on the veins.

Accessory wings are prominent on veins, leaving no room to place any intermediate between presence and absence of this feature (Fig. 10). The cells composing the accessory wings are quite the same as those of laminar surface in size, form, arrangement, and in structure of cell walls (Figs. 11 and 23). From this fact the accessory wings are considered to be the extra-outgrowths of the laminar surface in different levels from the usual ones. This kind of extra-expansion of laminar surface is unique to the filmy ferns but is not found in any other group of the megaphyllous plants.

Except in the case of *Amphipterum* among the filmy ferns, the same kind of accessory wings is found in *Dermatophlebium,* or *Hymenophyllum* subsect. *Plumosa* belonging to subgen. *Sphaerocionium,* although I know little of the eight species belonging to this and am not able to conclude here whether they form a single taxon or not. In addition, the accessory wings are various in occurrence: three New Guinean species have the accessory wings on the upper side of veins as well, while the west Malesian *H. fuscum* has the wings only on the lower surface of veins; or among eight species of *Sphaerocionium* two species have the accessory wings only on the lower surface and six others have the wings on both the surfaces. In all the cases the cellular construction of the wings is identical with that of the ultimate segments of the species concerned. In the cases of both *Dermatophlebium* and *Amphipterum,* I have no sufficient materials at hand to conclude whether each of them forms a distinct taxon or not, though it will be safely said that the feature is derived parallel to each other in the above two distinct groups.

'Scales' of *H. levingei* and *Buesia*

H. levingei has hardly been recognized for a long time in spite of appropriate description and figures given by Clarke (1880). On the lower surface of midrib of ultimate segments are the 'scales' attached to the axes longitudinally in two rows and hardly continuous with the next ones on the same row but imbricating to the opposite ones on the neighbouring row. The base of 'scale' is 3–7 cells in breadth and upper half consists of several cells arranging in one row and appearing as an articulated hair with larger apical cell of clavate outline (Fig. 12). The 'hairs' on the upper surface are longer than the hair-like portion of the 'scales' on lower surface, and they are articulated though not typically in construction with thin side walls and thick septae (Fig. 13). The cellular construction of the 'scales' is similar to that of laminar portion of ultimate segments (Figs. 14 and 15), so that the relationship between 'scales' and lamina is like that of accessory wing and lamina in *Amphipterum* and others. Moreover, it will be noted here that the 'scales' and 'hairs' are in two rows on both the upper and lower surfaces of midrib of ultimate segments, and this arrangement is comparable with that of the accessory wings in *Amphipterum.* From these facts, it will be suggested that the 'scales' and 'hairs' of *H. levingei* are the denticulation of the accessory wing, the laminar portion of such a wing being reduced in most cases.

The morphology of the scales is common between *H. levingei* and the species belonging to *Buesia.* In the latter the 'scales' are often longer, with longer apical cells. The arrangement is typically in two rows, imbricate, as easily seen by the naked eye.

Multi-directed projections and *Myriodon*

I have once referred Bornean materials to *Myriodon* (Iwatsuki, 1968) based solely upon the literature for the characteristics of the latter, but am doubtful at present to regard them as *Myriodon* which has peculiar projections on various lines of the axes of various orders. In *H. acanthoides* the marginal teeth are in various directions owing to the comprehensive crispature of segments and the reduction of laminar portion, though the midribs, or axes, are still continuously winged in this species with the base of projections in one line. Contrary to this the projections on axes are recorded to be not in one line in the case of *H. odontophyllum,* differing in this respect from the Bornean materials. The reduction of laminar surface is not particular among the filmy ferns as known in *Macroglena, Trichomanes setaceum* and others. When I referred the Bornean materials to

Myriodon I considered that the materials are in the extreme form in the series of *H. denticulatum* — *H. acanthoides* — *H. brassii,* represented by the reduction of laminar surface, though it is not probable if Copeland's observation was correct concerning *H. odontophyllum.*

The multi-directed projections of *Myriodon* may be speculated to have been resulted by the marginal denticulation and the splitting of accessory wing as schematically represented in Fig. 42. The teeth, or marginal projections, of segments and wings of *H. acanthoides* are similar to the projections of *Myriodon* and are also comparable with the 'scales' of *H. levingei* or of *Buesia,* which may be derived from the splitting of the accessory wing. In case the accessory wings are in double lines on both the surfaces, and the laminar parts as well as these accessory wings are split or reduced to remain as marginal teeth, the multi-directed projections will possibly be formed as in *Myriodon,* and the intermediate conditions are available as noted in the above description, although these 'conditions' do not necessarily represent the evolutionary intermediate but only the character phylogeny (Merkmalsphylogenie) is treated in this speculation.

2. INTERNAL CELL WALLS (plate II)

The internal walls of the laminar cells of *Meringium* are thick and coarsely pitted like those of *Selenodesmium* and some others belonging to *Trichomanes* s.l. Contrary to these cases, the internal cell walls of *Mecodium* and *Hymenophyllum* s.str. are generally thin and straight or slightly waved at most, though there are species which do not accord well with the definition of this feature of the taxa concerned. Among the species which belong to *Meringium,* those with thinner walls are: *H. armstrongii, H. blandum, H. bontocense, H. bivale, H. fejeense, H. macgillevirayi, H. multifidum,* and *H. viride.* Even in these species, the cell walls are not straight but more or less waved.

The thickness of the internal cell walls is also various among the species of *Meringium.* From the above observation, the difference in the structure of the cell walls is rather comparative, and not applicable to the difference in the taxa of higher rank, although a general tendency can be recognized as is treated such by various authors.

The cell walls of *Hymenophyllum* s.str. are usually described as thin and straight, as illustrated by Copeland (1937) except for *H. simonsianum.* In my observation, however, the cell walls are waved or pitted for all the species examined concerning *Hymenophyllum* s.str. The thickness is various according to the species, or even within the species for *H. barbatum* in which the southern form has thicker and more waved internal cell walls.

Most of the species of *Mecodium* have thin and straight internal cell walls, although there are several species with thick and coarsely pitted cell walls, such as: *H. crispato-alatum, H. exsertum, H. fimbriatum, H. flabellatum, H. javanicum, H. le ratii, H. montanum, H. oligosorum, H. opacum, H. riukiuense.* The distribution of the various forms of cell walls is similar to the case of *Meringium* and *Hymenophyllum* s.str., though the ratio of occurrence is different according to the 'genera'. From these facts, it is difficult to enumerate the structure of the cell walls as an important diagnostic feature to discriminate *Meringium* from the other groups belonging to *Hymenophyllum* s.l.

The contents of cells are variously illustrated by van den Bosch (1861), though they have to be observed in the living condition to evaluate the taxonomic significance. In this study the living materials were available only for a few species.

3. HAIRS ON RHIZOME AND FROND

The so-called articulated hairs are found on the upper surface of the axes in *H. levingei* and in *Buesia,* though this kind of 'hairs' is observed as to be identical with the 'scales' on the lower surface. The discussion on such 'hairs' has been given in the section on denticulation and is not appropriate to note in the section on hairs.

At the margin of the accessory wing on the veins in *Amphipterum,* there are the hairs identical with those found on the axes and rhizome of most species of *Meringium* and *Amphipterum.* The general morphology of this type of hairs is described in the foregoing pages in the section of general morphology. The basal cell of the hairs is attached to the axes or marginal cells of the accessory wing at the base or at the middle portion (Fig. 35) and the hairs are adpressed. Hairs of this type are also found in the species of *Hemicyatheon, Hymenophyllum* s.str., *Leptocionium,* and several species of *Mecodium.* In these species as well as in *Meringium,* the hairs are restricted to the axis and never observed at the margin of lobes. In this respect it is rather peculiar to observe the hairs at the margin of the accessory wing in *Amphipterum.* In some species of *Meringium,* the fronds are nearly glabrous, or the hairs are restricted to the very young portion of fronds and rhizome, though the structure of the hairs if any is the same in all the species belonging to the 'genera' cited above.

On the veins or especially at their junction, most species of *Mecodium* bear rather sparsely, small multicellular hairs consisting of several sub-transparent cells with thin walls (Fig. 39). This kind of hairs is quite different from the above described hairs found in *Meringium* and 'genera' allied to this. The stellate hairs of *Sphaerocionium* (Fig. 36) were observed in detail by Morton (1947) who applied the distribution of hairs to the subdivision of that 'section'. The stellate hairs are only known in *Sphaerocionium,* though the hairs of some species of *Microtrichomanes* were referred to the former hairs (Iwatsuki, 1975).

Marginal setae of *H. johorense, H. reductum,* and *H. armstrongii*

The morphology of *H. johorense* was well described by Holttum (1929, 1955) and Copeland (1937), although the marginal setae were illustrated only by the line drawing. The marginal setae are in two to six cells, with oblique septa giving hooked appearance of setae, dark brown, polished, with thick walls and pointed apex (Figs. 37–38). The setae are similar to those of *Trichomanes digitatum* group in appearance except for the multicellular construction in contrast with the unicellular setae of the latter. Similar setae are also found in *Didymoglossum* which belongs to *Trichomanes* s.l.

The fronds of *H. johorense* are small, simple to 5–6 lobed, branched nearly dichotomously, comparable to *Trichomanes digitatum* in this frond form, though this is also known in various dwarfed species as noted in the first part of this series. The margin of lobes is entire in *H. johorense,* not specialized except for bearing setae, the cell walls are thick and coarsely pitted, and the receptacles are extruded. We have no species of *Meringium* comparable to this species except for *H. reductum* and the systematic position of them is unknown at present. Copeland considered *H. johorense* as a member of *Microtrichomanes* but transferred *H. reductum* to *Meringium* without any reasonable interpretation.

H. armstrongii is a small fern in New Zealand, having the fronds simple to four-lobed, arranged subdichotomously or flabellately. Morton treated this species as a second member of subgen. *Craspedophyllum,* and his treatise seems to be probable considering only thin cell walls and deeply cleft bivalvate involucre, though the presence of marginal setae makes it doubtful to this conclusion. At margin of the ultimate segments of *H. armstrongii* are the setae of the same type as those of *H. johorense*. The marginal cells of the lobes are polished dark-brown, similar to the cell walls of the setae. In *Craspedophyllum,* however, the cells of a marginal row of the lobes are specialized without any marginal setae. The marginal cells of *H. armstrongii* are not specialized in structure, differing only in the dark-brown coloration. Anyway, it will be advisable at present to exclude *H. johorense, H. reductum,* and *H. armstrongii* from *Meringium* on the basis not only of the marginal setae but also of various other features.

4. Sorus

The position of sorus is paratactic in all the species in question. The involucre is obconic in the lower half with bivalvate upper portion. In this diagnosis the involucre is similar to that of *Crepidomanes* especially when pl. 16 of Copeland (1937) is compared with pl. 27 of Copeland (1933) as an example. The involucre of *Crepidomanes* is usually longer as a whole with longer tube and entire lips usually having the pseudoveins. In many cases the lips of involucre are denticulate at margin in *Meringium,* but the denticulation at lips of involucre is not in accordance with the denticulation at margin of segments and wings. On the surface of involucre, usually on the lower obconic part, there are the accessory projections in some species, especially in *H. denticulatum, H. acanthoides* and others. The depth of cleft is variable to some extent, and the obconic portion is either narrowly winged or not.

I have made a preliminary observation on the development of sorus in *H. polyanthos* and found that at first a small cup-shaped involucre is developed which becomes deeply cleft at maturity. Further observation is necessary to elucidate the character phylogeny of sorus.

The receptacles are clavate to cylindrical, growing indefinitely, and extruded from the lips of involucre. The form of receptacles is variable among the species of *Mecodium,* including capitate and clavate receptacles and longer involucre, but never extruded. The extrusion of the receptacles is various according to the species, although it will be notable that the exserted receptacles are found only for the sorus with obconic base. In *Mecodium* and *Hymenophyllum* s.str., the involucre is cleft nearly to the base forming no obconic basal portion, and the receptacles are never extruded even in the case when they are clavate in structure.

Hymenophyllum s.str. is discriminated from *Meringium* by the structure of sori, though the distinction is in some cases obscure. I have examined only a small number of specimens of American species, although I can point out that several species which are referred to *Meringium* have deeply cleft bivalvate involucre which forms a tube only at the basal portion. New Caledonian *H. dimidiatum* was included in *Meringium* by Copeland, and this is followed by Morton, as an isolated species, even with the description ‘receptacle, so far as seen, included’. Copeland noted that ‘sori . . . . cleft about half-way down’, though in fact the sori are deeply cleft nearly to the base and form obconic base when the sori are rather deeply placed at apex of the ultimate segments. From these facts, *H. dimidiatum* seems to be better placed in *Hymenophyllum* s.str. Contrary to that case, Australian *H. cupressiforme* is said to belong to *Hymenophyllum* s.str., by both of the above authors, though the receptacles are clavate and are larger, extruding in some cases from the lips of involucre. The small extrusion seems to depend upon the larger size of clavate receptacles, different from the long extruded receptacles typical for *Meringium.*

Classification of Meringium and 'genera' allied to this

It is recommended that all the species ever described be examined before proposing a system in the categories lower than family. In this study, however, the observation was made only for some representative species, pending the detailed comparison for every species concerned. The discussion on the system is, therefore, possible only in a limited sense, and a few comments will be made on the ever proposed systems.

Before the discussion on the relationship among the species of *Meringium* group, the systems proposed by Copeland and Morton will be summarized in a table:

Copeland (1947)

- I. Gen. 1 *Mecodium,* 2 *Craspedophyllum,* 3 *Hemicyatheon*
- II. Gen. 4 *Sphaerocionium,* 5 *Apteropteris,* 6 *Microtrichomanes*
- III. Gen. 7 *Hymenophyllum*
- IV. Gen. 8 *Meringium,* 9 *Amphipterum,* 10 *Myriodon,* 11 *Buesia,* 12 *Leptocionium,* 13 *Rosenstockia.*

Morton (1968)

- Gen. III. *Rosenstockia*
- Gen. IV. *Hymenophyllum*
  - Subgen. 1 *Hymenophyllum*: Sect. 1 *Hymenophyllum,* 2 *Buesia,* 3 *Ptychophyllum,* 4 *Eupectinum,* 5 *Myriodon*
  - Subgen. 2 *Sphaerocionium*: Sect. 6 *Sphaerocionium* (Subsects. *Ciliata, Plumosa, Hirsuta,* and *Leptocionium*), 7 *Apteropteris*
  - Subgen. 3 *Craspedophyllum*: Sect. 8 *Craspedophyllum*
  - Subgen. 4 *Hemicyatheon*: Sect. 9 *Hemicyatheon*
  - Subgen. 5 *Mecodium*: Sect. 10 *Mecodium* (Subsects. *Mecodium, Amphipterum,* and *Diplophyllum*).

1. MERINGIUM AND HYMENOPHYLLUM S.STR.

In definition *Hymenophyllum* s.str. is distinguished from *Meringium* 'by the more deeply cleft involucre, the shorter receptacle, the absence of peculiarly (pitted) thickened cell wall, and usually smaller size' (Copeland, 1838: p. 38). There are definitions by various authors, but the above seems to be a representative figuration. Morton cites the direction of sori for *Hymenophyllum* s.str., but this is true for only a few number of species.

Copeland (1938) enumerated 14 species for *Hymenophyllum* s.str. by his definition. One of them was transferred to sect. *Ptychophyllum* by Morton (1968) who added 11 species to sect. *Hymenophyllum* mostly following the suggestion given in the Index of Copeland (1938). I can not say exactly at present how many species belong to *Hymenophyllum* s.str., which may be classified into two: the group of *H. peltatum* represented by entire involucral lips include *H. antarcticum, H. perfissum, H. subdimidiatum,* and *H. wilsonii;* the other is the group of *H. thunbridgense* with denticulate involucral lips, including *H. barbatum, H. dimidiatum, H. revolutum,* and *H. simonsianum. H. cupressiforme* seems to belong to the former, though the lips are slightly dentate with shortly extruded receptacles, deeply cleft involucre, and thin but pitted internal cell walls. I have no sufficient knowledge on the southern species, although Copeland pointed out that the dwarfed species in the Far South, e.g. *H. minimum, H. pumilo,* and *H. pumilum,* were the representatives which were difficult to be distinguished between *Meringium* and *Hymenophyllum* s.str., the former two being actually included in sect. *Ptychophyllum* by Morton.

H. levingei has by far no direct relationship to *H. thunbridgense*. In having the 'trichomanes' on the axes of fronds, this resembles *Buesia*, though this particular feature may have been evolved independently in *H. levingei* and in *Buesia*. *H. levingei* is similar to *Buesia* in this feature but has entire margin of ultimate segments and deeply cleft involucre with clavate but not extruded receptacles. This species should be segregated from *Hymenophyllum* s.str., probably at the same level as *Buesia* from *Meringium*.

The cell walls are not distinctly different between *Meringium* and *Hymenophyllum* s.str., and the pale brown multicellular hairs are found in both of them. The sole feature to discriminate these two is the morphology of sorus, especially in the obconic base of involucre and extruded receptacles in the former. From these facts, *Hymenophyllum* s.str. and *Meringium* are considered to be close to each other accepting the system of Morton (1968) at least concerning this part.

2. Meringium and Mecodium

Morton included in sect. *Ptychophyllum* several species which were included in *Mecodium* by Copeland, e.g. *H. reinwardtii*, *H. samoense*, *H. taiwanense*, and *H. thuidium*. The interpretation in the structure of leaf margin was different between the above two authors. As noted in the previous pages in the section of denticulation, I prefer to follow Copeland keeping the above four species in *Mecodium*.

Among the Asiatic species of *Mecodium*, those of the group of *H. javanicum* is represented by waved or crisped margin of the ultimate segments and wings, thus representing the appearance similar to *Meringium*. Some of the species belonging to this group, e.g. *H. fimbriatum*, *H. javanicum*, and *H. riukiuense*, have denticulate lips of involucre and pitted internal cell walls. In these features they share the same characteristics with *Meringium*, though they appear to be identical as the result of the evolution along different courses.

H. macroglossum and *H. pachydermicum* were placed by Morton in sect. *Sphaerocionium* subsect. *Ciliata* 'without undue strain', contrary to the treatise of Copeland who included them in *Meringium*. As the hairs are quite different between *Sphaerocionium* and the other 'genera' belonging to *Hymenophyllum* s.l., we cannot accept the transferance by Morton as appropriate. We would refer to the fact that the above two species are close to some species with dense hairs belonging to *Mecodium*, e.g. *H. exsertum*, *H. gardneri*, and *H. oligosorum*, in hairiness, structure of internal cell walls, entire margin of segments, texture, coloration, and pinnation with broader wings giving the general appearance of shallow incision, but different only in the structure of sorus. The difference in soral construction is considered in this paper to record exactly the phylogeny among the species of the filmy ferns, though the pale brown multicellular hairs are common in *Meringium* and *Hymenophyllum* s.str. but not found in *Mecodium* except for the above species. *H. barbatum*, a representative of *Hymenophyllum* s.str., is also similar in appearance to the above mentioned species except for the denticulation at margin of segments and not so thick cell walls.

Morton noted that only four species of *Meringium* in the sense of Copeland had segments with entire margin but in fact the latter author included four more species without denticulate segment in the latter, and Morton enumerated these species in sect. *Ptychophyllum*. As noted in the section of denticulation, the entire margin is rather peculiar among the species of *Meringium*, but *H. penangianum* seems to be close to *H. holochilum* except for the entire margin of segments. *H. pachydermicum* and *H. macroglossum* are different in various features from *H. meyenianum*, but still belong to *Meringium* in the broader sense.

Morton distinguished *Ptychophyllum* and *Mecodium* in the level of subgenus, based chiefly on the structure of the margin of segment. In addition to the difference in denticulation, we can list up the difference in the structure of sorus and hairs between *Meringium* and *Mecodium,* admitting that the difference between them is comparatively smaller than the one between these two and *Sphaerocionium.*

3. THE 'GENERA' ALLIED TO MERINGIUM

Copeland gave a diagram of affinity of genera and showed that the close allies to *Meringium* were *Amphipterum, Buesia, Leptocionium,* and *Myriodon.* adding to them *Hemicyatheon* and *Rosenstockia* of doubtful relationship. In the opinion of Morton, on the contrary, the closest allies to *Meringium* are *Buesia, Hymenophyllum* s.str., *Myriodon* and a small group in South America named *Eupectinum.* He lowered the status of *Leptocionium* and *Amphipterum* to subsections under the subgenera *Sphaerocionium* and *Mecodium* respectively, that of *Hemicyatheon* to a distinct subgenus but retained *Rosenstockia* as a separate genus. Thus in his classification of the Hymenophyllaceae he admitted six genera.

Amphipterum. Morton considered that, only two species among four enumerated by Copeland, belonged to this taxon separating the other two on the basis of having the segmental margin denticulate. The systematic evaluation on denticulation has repeatedly been discussed in this paper which concludes that we can not distinguish any taxa of the filmy ferns in question based solely on this feature. I found no sound reason in the treatise of Morton and consider four, or three, species treated by Copeland are close to each other.

Thus confined, *Amphipterum* includes the species having the leaf margin denticulate or entire, although the accessory wing on veins not in the plane of the lamina is common to the species in question. The structure of sorus, hairs, internal cell walls, and the general appearance are not different between *Meringium* and *Amphipterum,* and it will be accepted here to keep *Amphipterum* as a distinct taxon very close to *Meringium.*

Buesia. Five species were referred to this by Morton (1968) who noted that he was uncertain that it even needed to be distinguished as a section. As was suggested by him, *Buesia* should better be compared with the species having the accessory wing, according to the speculation that the 'scales' may be the broken accessory wing.

Myriodon. The multi-directed projections of *Myriodon* were inferred as having been resulted from the occurrence of laminae in more than two planes and the splitting of laminar surface or reduction of lamina, remaining only the teeth. According to the above interpretation, that feature is particular, but *Myriodon* is quite similar to *Meringium* except for the above mentioned feature. *Myriodon* is accepted here as a monotypic taxon very close to *Meringium,* the conclusion being identical with that given by Copeland and by Morton.

Leptocionium. Indicated by the morphology of setae, this is considered as a relative of *Sphaerocionium* but not so close to *Meringium.* In this I prefer to follow not Copeland but Morton.

Hemicyatheon. This is recognized by Copeland on the basis of two species which were considered by him closely related to each other but had fallen into *Meringium* and *Mecodium* by definition, respectively. Morton maintained *Hemicyatheon* as a subgenus based on the type species, referring another species to subgen. *Hymenophyllum.*

H. deplanchei is not very close to *H. meyenianum,* though there is no problem to include the former in *Meringium,* especially by such features as denticulate margin of ultimate segments, thick and pitted internal cell walls, obconic involucre with denticulate lips cleft to the half-way, and exserted receptacles. Copeland's negotiation to place *H. deplanchei* in *Meringium* was based on his speculation that this species was close to *H. bailayanum* which was different from *Meringium* in entire margin of ultimate segments, although we refuse to separate any species from *Meringium* based solely on this feature. Judging from the soral structure and morphology of cell walls, *H. bailayanum* seems to belong to *Meringium* in broader sense, probably next to *H. deplanchei,* with the result again that the entire segment is not so particular to discriminate the taxa in a rank higher than species. Both Copeland and Morton consider that *H. bailayanum* is close to *Mecodium* and distinct from *Meringium* based on the entire margin of segments, although it is similar to *Meringium* in soral structure and cell walls which actually indicate the relationship among the species of the filmy ferns in question. Thus the two species included in *Hemicyatheon* by Copeland may better be transferred to *Meringium.*

Rosenstockia. I have little information to add to this monotypic 'genus', pending the further study when fresh materials are available.

4. SUBDIVISION OF MERINGIUM

There are several species groups separable from *H. meyenianum* and its close allies, although it is rather difficult to diagnose the groups within a few words. Moreover, there are several species which are included in *Meringium* by Copeland but are to be separated from this.

H. johorense, H. reductum, and *H. armstrongii* are distinct from *Meringium* in having dark brown marginal setae. As noted in the section of hairs, these three are distinct from the other members of *Meringium. H. johorense* and *H. reductum* form a small taxon not so far from *Microtrichomanes.* I have little information to add at present to *H. armstrongii* pending further investigation. It is doubtful that the latter is referable to *Craspedophyllum* as done by Morton.

Both *H. lobbii* and *H. blandum* are dwarfed species and apparently similar to each other, although it is difficult to know whether their resemblance is the result of parallel evolution or of the phylogenetic similarity. It is possible to recognize the similarity between these dwarf forms and the larger species without any actual evidence. I am sure that these species are not close to *H. johorense* and *H. reductum* irrespective of their apparent similarity.

H. pachydermicum and *H. macroglossum* form a group distinct from the others in having dense hairs on axes beneath, broader wings of axes and short entire segments which are broader towards base, giving an appearance of fronds less dissected, and brownish in dried condition. I have not seen actually the materials of *H. pulchrum* which seems to belong here by description and figure given by Copeland.

Many of the Southeast Asian species referred to *Meringium* are close to *H. meyenianum* having the characteristics described for typical *Meringium.* I am not sure at present whether the group of *H. holochilum* is separable from *H. meyenianum* group or not. *H. penangianum* and *H. edentulum* with entire or subentire margin of ultimate segments belong to the group of *H. meyenianum* in very strict sense.

I know little at present about the American species, and the southern species are still not observed in the living condition. *H. deplanchei* and *H. bailayanum* form a separate group even when they are included in *Meringium,* and no close allies can be represented here.

5. CONCLUSIVE REMARK

It is necessary to make a detailed revision of the species concerned before having a systematic conclusion of *Hymenophyllum* s.l., although it will be still useful to give here a system rather diagrammatically summarizing the above discussion for the basis of further investigation. This is a tentative scheme and is a modification of the systems given by Copeland and by Morton.

- *Hymenophyllum* s.l.
  - *Hymenophyllum*
    - *Hymenophyllum* s.str. (*Hymenophyllum* s.str. with two subgroups, *H. levingei,* and *Eupectinum*)
    - *Meringium* (*Meringium* s.str. with several subgroups, *Amphipterum, Buesia,* and *Myriodon*)
  - *Mecodium*
  - *Sphaerocionium*

References

van den Bosch, R. 1861. Hymenophyllaceae javanicae. Verh. kon Acad. Wetensch. Amsterdam IX–6: 1–67.

Clarke, C. B. 1880. A review of the ferns of Northern India. Tr. Linn. Soc. II. Bot. 1: 425–611.

Copeland, E. B. 1933. *Trichomanes*. Phil. J. Sci. 51: 119–280.

——— 1937. *Hymenophyllum*. Phil. J. Sci. 64: 1–188.

——— 1938. Genera Hymenophyllacearum. Phil. J. Sci. 1–110.

——— 1947. Genera Filicum. Waltham, Mass. 247 pp.

Holttum, R. E. 1929. New species of ferns from the Malay Peninsula. Gard. Bull. S.S. 4: 408–410.

——— 1955. A revised flora of Malaya II. Ferns of Malaya. Singapore. 643 pp.

Iwatsuki, K. 1968. Contributions to the classification of the filmy ferns (2). Acta Phytotax. Geobot. 23: 117–125, in Japanese.

——— 1975. Studies in the systematics of filmy ferns I. A note on the identity of *Microtrichomanes*. Fern Gaz. 11 (2 & 3): 115–124.

Morton, C. V. 1947. The American species of *Hymenophyllum* section *Sphaerocionium*. Contr. U.S. Nat. Herb. 29: 139–201.

——— 1968. The genera, subgenera, and sections of the Hymenophyllaceae. Contr. U.S. Nat. Herb. 38: 153–214.

Tagawa, M. 1940. Studies on Formosan ferns 2. Acta Phytotax. Geobot. 9: 139–148.

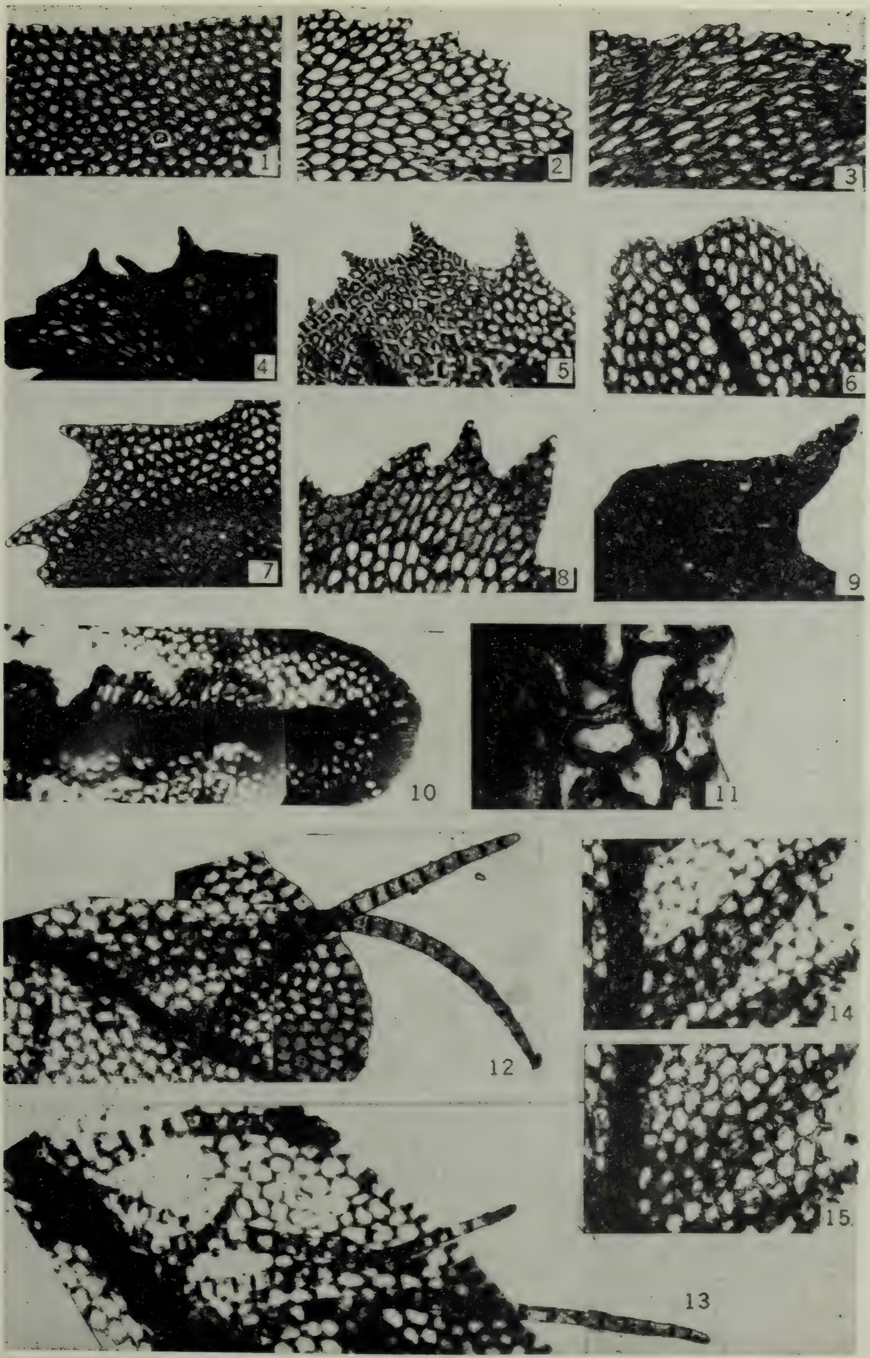


Plate I. Denticulation. Figs. 1–9. Margin of ultimate segment, × 100: Fig. 1, *H. polyanthos* (Iwatsuki et al. M 13034); Fig. 2, *H. taiwanense* (type); Fig. 3, *H. fimbriatum* (Tagawa 3347); Fig. 4, *H. barbatum* (Tagawa et al. T 1502); Fig. 5, *H. cupressiforme* (Muir 765); Fig. 6, *H. penangianum* (Mizutani 252245); Fig. 7, *H. meyenianum* (Iwatsuki et al. M 13549); Fig. 8, *H. denticulatum* (Iwatsuki et al. T 14579 bis); Fig. 9, *H. acanthoides* (Iwatsuki et al. M 13235). Figs. 10–11. Accessory wing of *H. fuscum* (Iwatsuki et al. S 1063): Fig. 10, ultimate segment with accessory wing, × 100; Fig. 11, Accessory wing, × 400, compare with II-23. Figs. 12–15. 'Scales' and 'hairs' of *H. levingei* (Kanai et al. 8249), × 100: Fig. 12, 'scales' on lower surface; Fig. 13, 'hairs' on upper surface; Figs. 14 & 15, comparison of 'scales' and segment, with focus on 'scales' in 14 and on segment in 15.

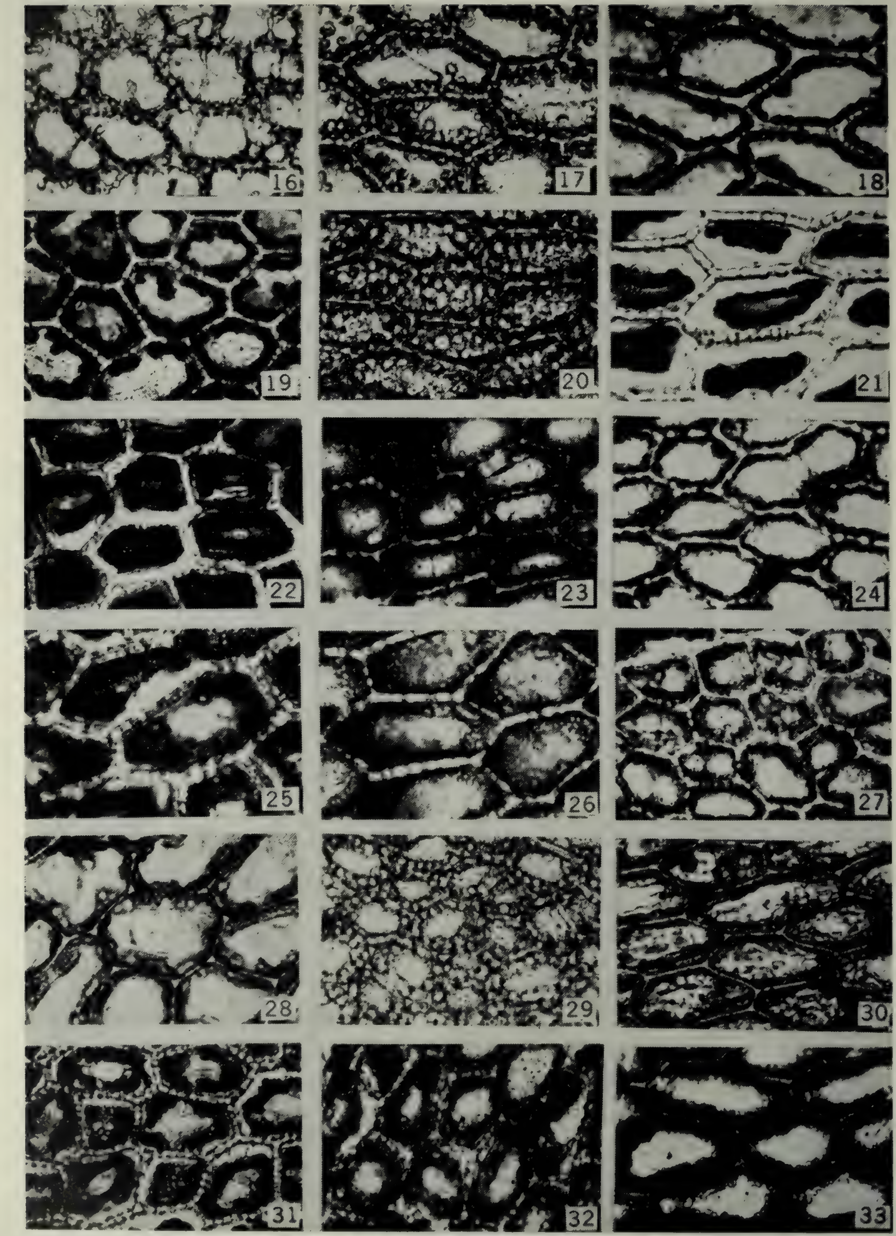


Plate II. Internal cell walls, all × 400: Fig. 16, *H. meyenianum* (Iwatsuki et al. M 13549); Fig. 17, *H. denticulatum* (Iwatsuki et al. T 14579 bis); Fig. 18, *H. blandum* (Iwatsuki et al. M 13515); Fig. 19, *H. multifidum* (Pichi Sermolli 6257); 20, *H. bontocense* (Tagawa et al. T 4815); Fig. 21, *H. johorense* (Mizutani 2724 a); Fig. 22, *H. deplanchei* (Balansa 1641); Fig. 23, *H. fuscum* (Iwatsuki et al. S 1063); Fig. 24, *H. barbatum* (Tagawa et al. T 1502); Fig. 25, *H. simonsianum* (Kanai et al. 725175); Fig. 26, *H. wilsonii* (Jermy et al. 8473); Fig. 27, *H. cupressiforme* (Muir 765); Fig. 28, *H. levingei* (Kanai et al. 8249); Fig. 29, *H. polyanthos* (Iwatsuki et al. M 13034); Fig. 30, *H. fimbriatum* (Tagawa 3347); Fig. 31, *H. oligosorum* (Iwatsuki 6657); Fig. 32, *H. exsertum* (Kanai et al. 725170); Fig. 33, *H. hirsutum* (Standley 21479).

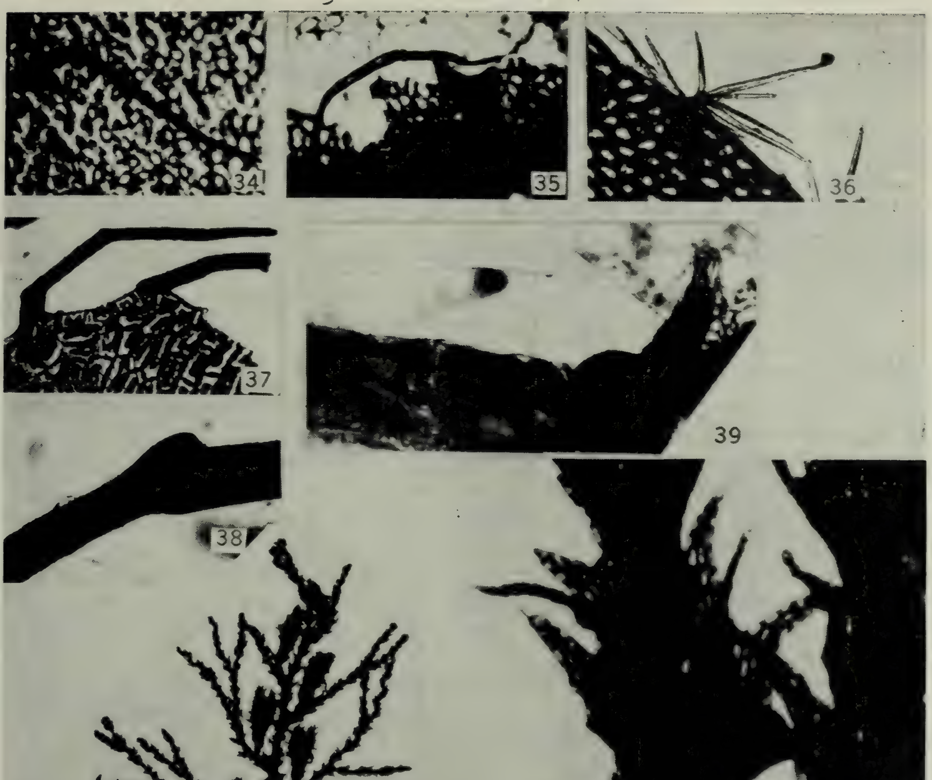
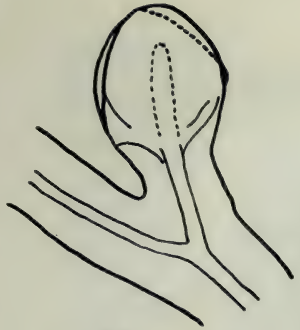


Plate III. Hairs and denticulation. Figs. 34–39. Hairs: Fig. 34, multicellular hair of *H. exsertum* (Kanai et al. 725170, × 100; Fig. 35, multicellular hair at margin of accessory wing of *H. fuscum* (Iwatsuki et al. S 1063), × 100; Fig. 36, stellate hairs of *H. hirsutum* Standley 21479), × 100; Fig. 37, marginal setae of *H. johorense* (Mizutani 2724 a), × 100; Fig. 38, oblique septa of Fig. 37, × 400; Fig. 39, multicellular hair of *H. polyanthos* (Iwatsuki et al. M 13034), × 400. Figs. 40–41. *H. acanthoides* (Iwatsuki et al. M 13235): Fig. 40, a plant, × 5; Fig. 41, segment with crisped denticulation, × 100.



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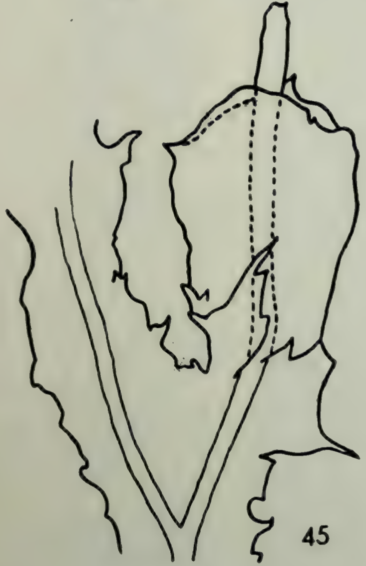

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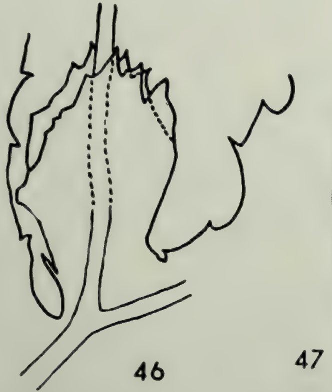

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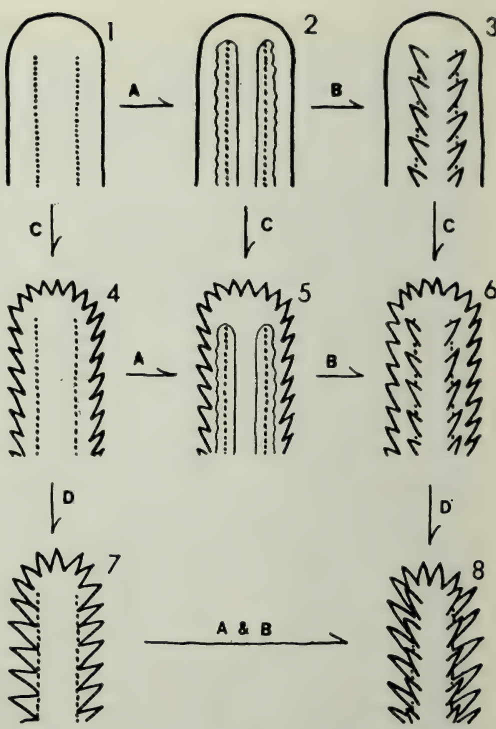

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Plate IV. Sorus and denticulation. Figs. 42–47. Line drawings of sorus: Fig. 42, *H. polyanthos;* Fig. 43, *H. barbatum;* Fig. 44, *Trichomanes digitatum;* Fig. 45, *H. denticulation;* Fig. 46, *H. hosei;* Fig. 47, *H. pilosissimum.* Fig. 48. Hypothetical scheme for a character phylogeny concerning the denticulation: *A*, development of accessory wing; *B*, splitting of accessory wing; *C*, denticulation of ultimate segment; *D*, reduction of laminar portion remaining only the teeth; 1, *Mecodium;* 2 & 5, *Amphipterum;* 3, *H. levingei;* 4 & 7, *Meringium;* 6, *Buesia;* 8, *Myriodon.*

Calamus caesius *and* **Calamus trachycoleus** *Compared*

by

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Summary

Two closely related rattan palms, *Calamus caesius* and *C. trachycoleus* are shown to have remarkably different habits; the silvicultural significance of the difference in habit is discussed.

Throughout the Lower Barito area of South Kalimantan, Indonesian Borneo, a rattan species receives intensive cultivation. This species, *Calamus trachycoleus,* is the only species cultivated on a large scale (i.e. thousands of hectares). It is closely related to *Calamus caesius* which also receives some degree of cultivation in the area and elsewhere. Though so similar to *Calamus caesius, C. trachycoleus* differs in one feature of its growth form; this difference has a major effect on the habit of the rattan and is one of the most important features of the species which has led to its ultimate supremacy as a plantation rattan. Holttum (1955) in his classic paper on growth forms of monocotyledons has indicated the importance of an understanding of the basic growth forms of monocotyledons; here is an example from the rattans where a difference in the degree of growth of one feature of a basically similar growth pattern differentiates between two species and accounts for the economic success of one over the other in cultivation.

DESCRIPTION OF THE GROWTH FORMS OF *CALAMUS CAESIUS* AND *C. TRACHYCOLEUS*

Calamus caesius Blume

This rattan is very widespread being found in Sumatra, the Malay Peninsula including Southern Thailand, and Borneo, at altitudes ranging from near sea-level in coastal peat swamp forest to 1000 m or more in the hills; the wide range may in part be due to the fact that it receives a rudimentary cultivation and is sometimes planted in primary forest near villages (Dransfield pers. obs. and hearsay from villagers in Borneo). It also seems to tolerate a great range of soil conditions from seasonally flooded alluvial clay soils, peat-swamp soils to well-drained steep soils on varying substrata in Hill Dipterocarp Forest. It is however commonest as a lowland plant on alluvial flats beside rivers. Throughout Borneo, the indigenous people often plant a few clumps of this and occasionally other species at the edge of their villages or near their longhouses. *Calamus caesius* without doubt produces the best quality small diameter class (7–15 mm) cane of all rattan species entering the rattan trade.

Calamus caesius produces rather dense clumps of many aerial stems, often more than 15 in number radiating from a condensed system of short underground rhizomes. Initial growth of the seedling produces an orthotropic stem about 1 cm in diameter including the leafsheaths. This seedling stem branches from the basal nodes to produce one to three sucker shoots which are also orthotropic; subsequent suckering from these sucker shoots produces short subterranean rhizomes c 3 cm in diameter and up to 10 cm long which bear pale brown scale leaves and short condensed internodes. Such rhizomes eventually (growth rates of the rhizomes are not known) metamorphose into rapidly growing orthotropic shoots of diameter 1.5 – 2.5 cm including the leaf-sheaths with lower internodes 50–100 cm or more in length bearing at the base leaves with highly reduced laminae often consisting of rachis alone and long-sheathing bases. Subsequent leaves develop more and more leaflets until the adult leaf shape is attained with the rachis bearing 10 or more grouped leaflets on each side, the rachis tip terminating in a cirrus. As the rhizome metamorphoses into an orthotropic stem, the two nodes at the area of metamorphosis each develop a branch with the potential of continued rhizomatous growth though the potential may not always be realised. Some of the branches remain dormant as bulb-like shoots. As each rhizome grows into an aerial stem, there is the potential for replacement by two new rhizomes and hence exponential increase in the number of aerial stems in the clump. However, because of the shortness of the rhizomes, many of the potential new rhizomes become juxtaposed and squashed and in this condition remain as bulb-like dormant shoots as described above. Further development of these dormant shoots depends on the opening up of the clump either effected by death of orthotropic shoots or by clearance by man of debris during cultivation of this species (pers. comm. from villagers in Borneo).

CALAMUS TRACHYCOLEUS BECC.

This rattan is only known from South Borneo within the watersheds of the rivers flowing into the Java Sea — i.e. the Barito, Kapuas (Kalimantan Tengah), Kahayan, Mendawai, Sampit and Seruyan Rivers. In this area it is found growing on seasonally-flooded riverbanks on alluvial clays and the margins of swamp forest. It receives intensive cultivation in the Barito Selatan area upriver from Kuala

1. The base of a clump of *Calamus caesius* with most roots removed; note the short rhizomes, bulb-like dormant shoots, and the smaller diameter of the aerial shoots compared with that of the rhizomes. (*Dransfield 3933*, Sungei Jaya, Kalimantan Tengah, 4.2.1974)

Kapuas on the Barito River, being grown in plantations on riverside seasonally-flooded alluvial soils. Though eminently successful as a plantation crop and in the wild, apparently, as a riverbank colonizer, it is unknown elsewhere in Borneo. *Calamus trachycoleus* produces a small diameter class cane (7–15 mm) with internodes generally shorter than those of *Calamus caesius* and of not quite such good quality; yet it accounts for about 80 per cent of the rattan trade on the Barito River.

Calamus trachycoleus is immediately distinguishable from *C. caesius* in producing diffuse open colonies rather than dense clumps; rather than having a condensed system of short underground rhizomes, it spreads by means of lax above-ground stolons. Initial growth of the seedling is similar to that of *C. caesius*, the first stem and one or two suckers being orthotropic. Subsequent branching results in robust stolons up to 4 cm in diameter which grow along the soil surface or slightly raised above ground level on short adventitious roots. The stolons (known locally as "selantar") bear sheathing pale brown scale leaves and short internodes 4–7 cm long and like the rhizome of *C. caesius* metamorphose into orthotropic stems. The length of the stolons from point of origin to point of metamorphosis may be 3 m or more. As in *Calamus caesius*, two branches are produced at the area of metamorphosis, one each from adjacent nodes, but unlike *C. caesius*, both branches grow out to produce new stolons unless damaged; no dormant branches have been observed and this is regarded as being correlated with the open growth of the clump and apparent lack of competition between the branches.

Each branch in *Calamus trachycoleus* is apparently adnate to the internodes of the proceeding leaf and is hence carried out of the scaleleaf axil; however their position suggests an axillary origin rather than an internodal or other anomalous origin. This feature of *Calamus trachycoleus* deserves anatomical investigation. Of the two branches produced at each metamorphosis, the proximal tends to develop before the distal and may be already 30 cm in length before the distal emerges

2. A piece of a stolon ("selantar') of *Calamus trachycoleus* at the point of metamorphosis into an orthotropic; stem sheaths have been removed to show the production of two branches at the point of metamorphosis. *Dransfield 3929*, Sungei Jaya, Kalimantan Tengah 4.2.1974).

from the scale leaves. Because of distortion the proximal branch of the stolon appears to continue the growth of the subtending stolon and at first sight the orthotropic stem appears as the branch rather than the main axis. If young material is examined at a stage when a stolon tip begins to grow upwards, the two new stolons are seen to be branches rather than one of them being a continuation of the stolon.

Unlike *Calamus caesius, C. trachycoleus* is a rapidly invasive species and the potential of exponential increase in number of aerial stems is usually realised. Once a plantation of *C. trachycoleus* has been established very little cultivation is necessary and harvests can be made after an initial 7–10 year period at 2 yearly intervals. In *C. caesius* on the other hand, clumps require clearance of debris to encourage development of new shoots and in the Barito Selatan area of South Borneo at any rate, only two main harvests are obtained, an initial one after 7–10 years followed by a second after a further four years; after the second harvest the clumps are supposedly exhausted.

DISCUSSION

In his original description of *Calamus trachycoleus* Beccari (1913) comments that the rattan is allied to *C. caesius* but most closely related to *C. pogonacanthus*. Recent fieldwork in Borneo has allowed the present author to make several collections of *C. pogonacanthus* which is now seen to belong to a distinct group of species in *Calamus* all with the peculiar feature of bearing both a cirrus and a flagellum. Cirrus (barbed whip at the end of the leaf representing an extension of the leaf rachis) and flagellum (barbed whip borne on the leaf sheath and representing a sterile inflorescence) are the two major climbing organs found in Malesian rattans and are usually mutually exclusive. The presence of both in *C. pogonacanthus* and a few other species is hence noteworthy. *C. trachycoleus* bears a cirrus only and hence is here regarded as being more closely related to *C. caesius* than to *C. pogonacanthus*. Furthermore, in the field, without reference to the remarkable difference in habit, *C. caesius* and *C. trachycoleus* are distinguished with some difficulty — both species are about the same size, have very similar leaflet arrangement, and have white indumentum on the lower leaflet surfaces, though in *C. trachycoleus* it is sparse and usually only present on young leaves. The leaf sheath with its abundant minute thorns forming a scabridity between the sparse large triangular thorns in *C. trachycoleus* and lacking such scabridity in *C. caesius* is the only reliable character for distinguishing the two species in the herbarium; yet in the field the two are seen to be remarkably distinct because of their differing habits.

The striking differences in development of the suckering habit of these two rattans illustrates how important such differences may be to the silviculturalist; further studies of rattan suckering habits may produce other examples of closely related species differing in habit and are seen to be of great importance in a consideration of the ecology of rattans.

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REFERENCES

BECCARI, O. (1913): Asiatic Palms — Lepidocaryeae, Part 1 The species of *Calamus*. Appendix. *Ann. R. bot. Gard. Calcutta* **11**.

HOLTTUM, R. E. (1955): Growth habit of monotyledons — variations on a theme. *Phytomorphology* **5** (4), 399–413.

Synaptospory: a hypothesis

A possible function of spore sculpture in pteridophytes

by

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Summary

Part of the spore output of some ferns is shed in groups of spores, sometimes still contained within the sporangium. It is theorized that spore sculpture, particularly a distinct, strongly sculptured perispore, plays a part in keeping, or bringing, spores together. This is important for increasing the chance for intergametophytic fertilization. The want of a pronounced spore sculpture in most epiphytic ferns and the strongly sculptured spores of heterosporous pteridophytes are brought in connexion with the phenomenon, tentatively called synaptospory.

Until recently, pteridologists used to distinguish between fern taxa (genera or groups of higher rank) with a perispore and taxa without one, and much taxonomic value was attributed to this character (e.g., Kramer in Lanjouw & collab., 1968; Wagner, 1974). Through Lugardon's fundamental work (e.g., 1971, 1972a, 1974) it has now become known that the perispore is apparently of universal occurrence in ferns, and it has also been found in so-called fern allies (e.g., Lugardon 1969, 1972b, 1973). It is therefore no longer correct to speak of ferns with and ferns without a perispore. Instead, one should distinguish between spores having a perispore that is firmly appressed to the exospore, and others where the perispore forms a distinct, usually strongly sculptured layer. To avoid this awkwardness in expression I shall continue to speak below of spores with and spores without a perispore, being, of course, fully aware of the incorrectness of these terms.

In most cases a strongly developed surface sculpture of a spore was attributed to the perispore although in some cases the exospore was held responsible for the surface features. It now seems as if in all these cases a perispore is present, but where it seemed to be absent it firmly adheres to the exospore and cannot readily be distinguished except in cross-sections examined with the transmission electron microscope.

Whatever the morphological interpretation, the function of this surface sculpture has remained a matter of conjecture, not to say an enigma, as it remains to this day, to a certain extent and largely as to details, in the pollen grains of seed plants. In the following I want to put forward a hypothesis that tries to account for the presence of spore sculpture in pteridophytes. I wish to stress that it may only be one of several possible functions, and that the attempt at an explanation is no more than a hypothesis, as for the moment it rests on too few observational data. I hope, though, that it may lead to further experimental work and will either be confirmed or, if disproved, will show to have been a stimulating error.

When we review the "presence" or "absence" of a perispore (inverted commas because of the restrictions stated above), or, more generally, of a pronounced external sculpture in the spores of modern ferns, it becomes immediately apparent that large groups are without such sculpture and other, equally large and as a rule very naturally defined ones, possess it. Wagner (l.c.) regarded the groups with a pronounced perispore as derived ones, and the perispore in general as a specialization, whatever its function. It seems to me that there is another striking correlation, namely between the "presence" or "absence" of a perispore and the habitat of the fern, that has, to my knowledge, not been reported before.

If we regard the spore wall of taxa of higher order among the modern ferns, it springs to the eye that epiphytic genera, genus groups, etc., in most cases have more or less smooth, "perisporeless" spores: Vittarioids, Davallioids, Grammitidoids, Polypodioids, Hymenophyllaceae. Minor exceptions can be found with ease, e.g. in the Polypodioids in *Drymoglossum* (see Wagner, l.c., fig. 2), in the Davallioids in *Gymnogrammitis* (see Ching, 1966, and Sen & Sen, 1971), etc., and there is one important major exception: the genus *Elaphoglossum*. This, though containing some terrestrial species, as do indeed most epiphytic groups, consists almost entirely of epiphytes; but its alliance is with a group of terrestrial or scandent genera known as the Lomariopsidoid ferns or Lomariopsidaceae*). "Perispore-less" spores occur, of course, in a considerable number of essentially or entirely terrestrial fern groups. Examples are Osmundaceae, Plagiogyriaceae and Dennstaedtioids.

A second observation, of high relevancy in this context, was recently published by Schneller (1975). It has nearly always been assumed, explicitly or tacitly, that fern spores are scattered invidually as far as possible. Schneller showed that in *Dryopteris* spp. a not inconsiderable part of the spores is shed in groups of two, three, four, or more.

According to Gastony's findings (1974), in certain tree-ferns not the spore but the sporangium, with its complete spore-content, is the unit of dispersal. The spores germinate whilst held together by the sporangium. I have the strong impression that at least partial retention of spores in the sporangium, with subsequent shedding of the entire structure, is not a rare phenomenon in ferns.

The pioneer work by Näf (1961) and Voeller (1971) has shown that the development of gametophytes and their sex organs is a process subject to physiological interaction between closely associated prothalli. These interactions greatly tend to favour intergametophytic fertilization and hence gene exchange. Various authors have reported on the much greater viability of fern sporophytes produced by intergametophytic as opposed to intragametophytic fertilization (e.g., Lloyd, 1974).

Terrestrial ferns by and large may be supposed to grow in an essentially stable environment (there are, of course, exceptions like pioneers on bare soil, lava flows, etc.) where the rate of mortality of individual plants is relatively low. Once they are mature, individual plants often grow slowly and are supposed to be potentially very long-lived, e.g., in *Osmunda regalis*. Except when new habitats are colonized, sexually produced new generations will follow each other at rather long time intervals, and it must be of great importance for the plants to maintain their genetic variability, and to avoid the influence of recessive deleterious genes, by increasing the chance for cross-fertilization when new plants are sexually produced from prothalli. The coherence of some spores, whether through the action of the spore wall or by retention in the sporangium, must greatly enhance this chance, and external spore sculpture may be one mechanism by which the former is achieved. Spores from one sporangium will not be all genetically identical, unless the mother plant is one hundred percent homozygous. Schneller (l.c.) found many groups of more than four spores being dispersed as a unit, so the tetrad is certainly not the

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* On the evidence available at present I find myself unable to agree with Tutin (1964) and Pichi Sermolli (1968) who distinguish a family Elaphoglossaceae comprising only *Elaphoglossum* and satellite genera.

limit beyond which the spores do not cohere. And there seems no reason to suppose why spores produced by different plants from one colony, and even from different ones, could not meet after having been dispersed by air currents, runoff water, etc., for instance, in a surface-film of rainwater, cohere, and germinate together, with subsequent cross-fertilization.

In contrast, most epiphytes inhabit a very unstable *milieu*. The branches and twigs they colonize have but a limited life-span, and they are thus bound to colonize new places continuously in order to survive as a species. Many do this by producing long-creeping, branching rhizomes, or sometimes runners, and such ferns very often inhabit the smaller branches and twigs of trees and shrubs, as I observed myself in some parts of tropical America, and as can be deduced from de la Sota's diagram (1971, fig. 13) illustrating Costa Rican fern epiphytes; see also Johansson (1974). The epiphytes with short rhizomes, often more massive, or even forming so-called nests, favour the more stable habitats of the main trunks and crotches of larger branches.

For colonizing new stations, these, as it were, pioneer epiphytes thus depend to a great extent on spore dispersal, which must be sufficient and efficient in order to ensure maintenance of a sufficiently large population, in spite of considerable turnover. This must largely be achieved by dispersing individual spores, and self-fertilization in lone prothalli originating from singly spread spores should be much more common in these plants. Indeed, coherence of spores in groups would impede dispersal. Wagner (l.c.) suggested that the lack of a perispore in Davallioid ferns should be regarded as a result of secondary loss of this organ, and if that is true, it might be regarded as an adaptation to epiphytism. With the comparatively rapid succession of sexually produced generations, occasional cross-fertilization would suffice for maintaining genetic variability.

In this connexion it is, I think, significant that so very few natural hybrids of epiphytic fern species have been reported, in contrast to the many terrestrial hybrids known. This may be due in part to the physical inability of the researcher to sample populations of epiphytes in the same way as of terrestrial or epilithic species, but it can hardly account for the fact as a whole. The regular development of single, self-fertilized prothalli may well be the reason for a greatly reduced chance for interspecific cross-fertilization.

The phenomenon of coherence of spores by means of cohering or interlocking surface structures may be called "synaptospory", analogous to what has been called "synaptospermy" in seed plants, after Murbeck (see, for instance, Zohary, 1962, p. 180, and van der Pijl, 1969, p. 77). Further research will have to show whether it exists as a widespread phenomenon.

One general feature observed in terrestrial heterosporous lycopodiophytes seems to point in the same direction. The great majority of *Selaginella* species, and many species of the partly terrestrial genus *Isoetes,* have strongly sculptured spores. For illustrations, see, for instance, Knox (1950) and Hellwig (1969). For sexual reproduction these plants are, of course, entirely dependent on germination of spores producing gametes of opposite sex in very close proximity. The surface sculpture may here, too, serve to enhance the chance for this to occur.

Equisetum is probably another case in point. The perispore here dissolves into hygroscopically moving bands, somewhat unfortunately termed elaters, which loosen the spore mass but also become entangled, leading to distribution of spores in groups. The prothalli are at least very often functionally unisexual (Sporne, 1952, p. 112; Duckett & Duckett, 1974).

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References

Ching, R. C. 1966. Gymnogrammitidaceae Ching, a new fern family. *Acta Phytotax. Sin.* **11**: 11–16.

Duckett, J. G., & Duckett, A. R. 1974. The ecology of Equisetum gametophytes. *Am. J. Bot.* **61**: 36 [brief report].

Gastony, G. J. 1974. Spore morphology in the Cyatheaceae. I. The perine and sporangial capacity: general considerations. *Am. J. Bot.* **61**: 672–680.

Hellwig, R. L. 1969. Spores of the heterophyllous Selaginellae of Mexico and Central America. *Ann. Missouri Bot.* G. **56**: 444–464.

Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr. Suec.* **59**: 1–129.

Knox, E. M. 1950. The spores of Lycopodium, Phylloglossum, Selaginella and Isoetes, and their value in the study of microfossils of Paleozoic age. *Trans. Bot. Soc. Edinb.* **35**: 211–357; 12 plates.

Kramer, K. U. 1968. Pteridophyta, in: J. Lanjouw & collab. *Compendium van de Pteridophyta en Spermatophyta.* Oosthoek, Utrecht. 342 pp.

Lloyd, R. M. 1974. Genetic and mating system studies in ferns: systematic and evolutionary implications. *Internat. Organiz. Plant Biosyst. Newsletter* **9**: 2–14.

Lugardon, B. 1969. Sur la structure fine des parois sporales d'Equisetum maximum Lamk. *Pollen et Spores* **11**: 449–474.

———— 1971. *Contribution à la connaissance de la morphogénèse et de la structure des parois sporales chez les Filicinées isosporées.* Thèse, Université de Toulouse. 257 pp., 51 plates.

———— 1972a. La structure fine de l'exospore et de la périspore des Filicinées isosporées. I — Généralités. Eusporangiées et Osmundales. *Pollen et Spores* **14**: 227–261.

———— 1972b. Sur la structure fine et la nomenclature des parois microsporales chez Selaginella denticulata (L.) Link et S. selaginoides (L.) Link. *C. R. Acad. Sci. Paris Sér.* D **274**: 1656–1659.

———— 1973. Nomenclature et structure fine des parois acétorésistantes des microspores d'Isoetes. *C. R. Acad. Sci. Paris* Sér. D **276**: 3017–3020.

———— 1974. La structure fine de l'exospore et de la périspore des Filicinées isosporées. II. Filicales. Commentaires. *Pollen et Spores* **16:** 161–226.

Näf, U. 1961. Mode of action of an antheridium-inducing substance in ferns. *Nature* 189: 900–903.

Pichi Sermolli, R. E. G. 1968. Adumbratio Florae Aethiopicae 15. Elaphoglossaceae. *Webbia* **23**: 209–246.

van der Pijl, L. 1969. *Principles of dispersal in higher plants.* Springer-Verlag, Berlin. 154 pp.

Schneller, J. 1975. Untersuchungen an einheimischen Farnen, insbesondere der Dryopteris filix-mas-Gruppe. 3. Teil. Oekologische Untersuchungen. *Ber. Schweiz. Bot. Ges.* **85**: 110–159.

Sen, T., & Sen, U. 1971. Morphology and anatomy of the fern genus Gymnogrammitis. *Ann. Bot.* **35**: 229–235.

de la Sota, E. R. 1971. El epifitismo y las pteridófitas en Costa Rica (América Central). *Nova Hedwigia* **21**: 401–465.

Sporne, K. R. 1962. *The morphology of pteridophytes*. Hutchinson, London. 192 pp.

Tutin, T. G. 1964. *Elaphoglossaceae*, in: T. G. Tutin, V. H. Heywood & collab., *Flora Europaea* Vol. I. Cambridge. xxxii + 464 pp.

Voeller, B. 1971. Developmental physiology of fern gametophytes: relevance for biology. *BioScience* **21**: 266–270.

Wagner, W. H. Jr. 1974. Structure of spores in relation to fern phylogeny. *Ann. Missouri Bot. G.* **61**: 332–353.

Zohary, M. 1962. *Plant life of Palestine*. Ronald Press, New York. 262 pp.

Spore Morphology of Malayan Dennstaedtiaceae *sensu* Holttum

by

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Abstract

Spore morphology of 28 species belonging to 28 genera included by Holttum (1954) in the Dennstaedtiaceae are described. Amongst the Malaysian taxa there are at least seven distinct spore-types. The disposition of the Malaysian genera in these spore-types does not conform with any of the existing systems of classification. Only spores of those genera assigned by Holttum in the subfamilies Davallioideae, Dryopteridoideae and Tectarioideae show some degree of uniformity.

Introduction

The Dennstaedtiaceae as originally defined by Holttum (1947, 1949, 1954) is a very large family of modern ferns, containing very diverse groups of genera and species. In the Peninsular Malaysia alone the family comprises not less than 48 genera and 203 species out of the total 124 genera and 389 species of its fern-flora. As has been shown in the excellent review by Pichi Sermolli (1973) and Mickel (1973), there seems to be a great controversy over the delimitation and classification of the taxa involved. Many authors, such as Christensen (1938), Ching (1940), Copeland (1947), Reimers (1954), Pichi Sermolli (1958), Nayar (1970) and others placed the 48 Malaysian genera involved in 5 or 10 separate families, whereas Holttum (1954) included these genera in 11 subfamilies of the Dennstaedtiaceae, though later (1973) he more or less agrees with Pichi Sermolli's system of classification. Furthermore, it is also evident that there is a great difference of opinion with regard to the disposition and affinity of the genera within each family or subfamily recognised by the above authors.

In an attempt to introduce a more natural system of classification of these taxa, many pteridologists (e.g. Atkinson, 1973; Lovis, 1973; Manton, 1961; Mickel, 1973; Sen & Sen, 1973; Sledge, 1973; Swain & Cooper-Driver, 1973; Van Cotthem, 1973; Walker, 1973, and others) have used modern and advanced techniques in their studies, previously unexploited by those who are responsible in drawing up the existing schemes of classification. Amongst these modern techniques are: anatomical, cytological, phytochemical, biochemical, developmental and palynological.

Of the palynological aspects, Erdtman & Sorsa (1971) have admirably summarised our present knowledge on the spore morphology of those genera included in the Dennstaedtiaceae by Holttum. This work shows that of the total 3052 species so far recognised in the 48 genera occurring in Malaysia (Willis, 1973), spore descriptions of only 449 (= 14.7%) have been published by Harris (1955), Erdtman (1957), Nayar & Devi (1963, 1964a, 1964b, 1966, 1967, 1968a, 1968b), Nayar & Kaur (1963), Tardieu-Blot (1963a & b, 1965), and several others. Of these descriptions only a few were based on Malaysian specimens.

The present paper describes the spores of 28 species belonging to 28 genera, and is intended as a starting point for more intensive works to be done in the future.

Species Investigated

1. DENNSTAEDTIOIDEAE
   Hypolepis bivalvis v.A.v.R.
   Microlepia speluncae (L.). Moore
   Orthiopteris kingii (Bedd.) Holtt.

2. LINDSAEOIDEAE
   Isoloma divergens (Hook. f. & Grev.) Sm.
   Lindsaea scandens Hook. f.
   Sphenomeris chusana (L.) Copel.
   Tapeinidium pinnatum (Cav.) Christ.

3. DAVALLIOIDEAE
   Davallia divaricata Bl.
   Humata heterophylla (Sm.) Desv.

4. OLEANDROIDEAE
   Nephrolepis biserrata (Sw.) Schott.
   Oleandra pistillaris (Sw.) Christ.

5. PTERIDIOIDEAE
   Acrostichum aureum L.
   Histiopteris stipulacea (Hook. f.) Copel.
   Pteris vittata L.
   Stenochlaena palustris (Burm.) Bedd.

6. ASPLENIOIDEAE
   Asplenium nidus L. var. *musifolia* (Sm.) Bedd.

7. BLECHNOIDEAE
   Blechnum orientale L.
   Brainea insignis (Hook. f.) Sm.

8. LOMARIOPSIDOIDEAE
   Bolbitis heteroclita (Pr.) Ching
   Egenolfia appendiculata (Willd.) Sm.
   Elaphoglossum callifolium (Bl.) Moore
   Lomagramma sumatrana v.A.v.R.
   Teratophyllum aculeatum (Bl.) Mett. var. *montanum* Holtt.

9. DRYOPTERIDOIDEAE
   Dryopteris sparsa (Don) O. Ktze.

10. TECTARIOIDEAE
    Arcypteris irregularis (Pr.) Holtt.
    Heterogonium pinnatum (Copel.) Holtt.

11. ATHYRIOIDEAE
    Athyrium pinnatum (Blanco) Copel.,
    Cystopteris tenuisecta (Bl.) Mett.

Materials and Methods

In this study both fresh and herbarium materials were used. The fresh specimens were collected from various localities in Selangor and Pahang, and were identified with the help of Holttum's keys (1954). Voucher specimens are now deposited in the Herbarium, Department of Botany, University of Malaya, Kuala Lumpur (KLU). Dried and preserved materials were obtained from herbarium specimens available in the above Herbarium.

Spores containing materials were acetolysed, stained lightly with safranin, and mounted in glycerin jelly. The slides were then sealed permanently with paraffin wax. In some species, during acetolysis the perine was easily dissolved and the spores become shrivelled. In such cases, a lesser amount of concentrated sulphuric acid was added in the acetolysing mixture and heating was skipped. Although by this treatment, the spores did not become transparent, the perine remained intact and could be studied. Observation, measurement and photomicrography was carried out with a Leitz Dialux Microscope fitted with occular micrometer, Combiphot Automatic Camera System, achromatic condensor with N.A. 0.90, phaco achromatic objectives 40x /0.65 and 100X /1.30, and halogen lamp-housing model 100 Z.

For each species, measurement is based on 50 readings. This measurement is expressed in the text as length of polar axis (P) × longitudinal equatorial diameter (E1) × transverse equatorial diameter (E2) in monolete-bilateral spores and as P × E1 in trilete-tetrahedral spores. All measurements are exclusive of perine and any other processes.

Description of Spores

DENNSTAEDTIOIDEAE

1. *Hypolepis bivalvis* (Gunong Brinchang, Perak; Poore KLU 468; Plate 8, Figs. 4–7).

Spores monolete-bilateral, 30–46 × 48–61 × 33–46 μ. Amb oblong; proximal face flat, distal face hemispherical. Laesura 36–40 μ, margins thickened into protruding lips about 4 to 7 μ broad on either side of the laesura. Exine 2 μ thick, sexine thicker than nexine, with fine spinulose pattern. Perine thin and provided with minute spine-like processes.

2. *Orthiopteris kingii* (Cameron Highlands, Pahang; Turnau KLU 2936; Plate 2, Fig 8).

Spores trilete-tetrahedral, 29–32 × 31–39 μ. Amb triangular in outline, with convex sides and broadly rounded corners. Proximal face conical, distal face convex to hemispherical. Laesura 15 μ, margins thickened into lips about 3 μ broad and tapering towards the tips. Exine 2 μ thick, sexine nearly as thick as nexine, smooth. Perine absent.

3. *Microlepia speluncae* (Templer Park, Selangor; Abd. Samat b. Abdullah KLU 2686; Plate 2, Figs. 6–7).

Spores trilete-tetrahedral, 25–33 × 30–33 μ. Amb triangular with strongly concave sides and broadly rounded corners. Proximal face slightly convex to flat; distal face hemispherical. Laesura 13 μ, margin thickened into lips of 2 μ broad and tapering towards the tips. Exine 2 μ thick, sexine as thick as nexine, densely granulose. Perine absent.

LINDSAEOIDEAE

4. *Lindsaea scandens* (Gunong Ulu Kali, Pahang; Abd. Samat b. Abdullah KLU 1846; Plate 2, Figs. 2–3).

Spores trilete-tetrahedral, 22–25 × 24–27 μ. Amb triangular, with slightly convex to straight sides. Proximal face conical with angular pole; distal face convex. Laesura 13 μ, margins thickened into lips of 1 μ broad. Exine 1 μ thick, not clearly subdivided into sexine and nexine, densely granulose. Perine absent.

5. *Sphenomeris chusana* (Fraser's Hills, Pahang; Turnau KLU 2701; Plate 9, Fig. 3).

Spores monolete-bilateral, 43–63 × 65–76 × 40–51 μ. Amb oblong. Proximal face flat; distal face hemispherical. Laesura 51 μ, margins thickened into protruding lips of 8 μ broad. Exine 2 μ thick, sexine much thicker than nexine, smooth. Perine smooth and thin, partially peeling off on acetolysis.

6. *Isoloma divergens* (Genting Simpah, Selangor; Mohd. Kassim b. Rajab KLU 139; Plate 2, Figs. 4–5).

Spores trilete-tetrahedral, 19–22 × 20–25 μ. Amb triangular with straight to slightly convex sides and broadly rounded corners. Proximal face conical with angular pole; distal face convex. Laesura 12 μ, margins thickened into lips of 1 μ broad. Exine 1.5 μ thick, sexine much thicker than nexine, smooth. Perine-like layer present, smooth, very closely adherent to the exine, and disintegrates very easily on acetolysis.

7. *Tapeinidium pinnatum* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12307; Plate 9, Fig. 4).

Spores monolete-bilateral, 26–32 × 28–46 × 27–32 μ. Amb. oblong. Proximal face flat to slightly convex; distal face hemispherical. Laesura 32 μ, margins thickened into protruding lips of 6 μ broad. Exine 1.5 μ thick, sexine thicker than nexine, smooth. Perine thin with fine reticulate pattern, disintegrates easily on acetolysis.

DAVALLIOIDEAE

8. *Davallia divaricata* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12309; Plate 6, Figs. 1–3).

Spores monolete-bilateral, 27–35 × 36– 50 × 24–34 μ. Amb oblong. Proximal face concave; distal face convex. Laesura 28 μ, margins slightly thickened into lips of 2 μ broad. Exine 2.5 μ thick, sexine thicker than nexine, verrucose to rounded tuberculose; verrucae or tubercles crowded, 5–7 μ in diameter and 2 μ high. Perine absent.

9. *Humata heterophylla* (Lombong, Johore; Abd. Samat b. Abdullah KLU 1849; Plate 6, Figs. 4–8).

Spores monolete-bilateral, 22–36 × 38–43 × 28–32 μ. Amb oblong. Proximal face flat; distal face hemispherical. Laesura 18 μ, margins slightly thickened into lips of 1 μ broad. Exine 3 μ thick, sexine thicker than nexine, verrucose-tuberculose; tubercles crowded, round, 2 μ high, 5–7 μ broad and 10–16 μ long. Perine absent.

OLEANDROIDEAE

10. *Oleandra pistillaris* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12310; Plate 4, Figs. 5–6).

Spores monolete-bilateral, 19–26 × 27–32 × 17–23 μ. Amb oblong. Proximal face flat; distal face hemispherical. Laesura 17 μ, margins slightly thickened into lips of 1 μ broad. Exine 4–5 μ thick, sexine thicker than nexine, smooth. Perine loosely wrinkled, anastomosing to form a reticulate patterns; folds about 4 μ high, spinulose; spinules minutes, less than 1 μ high, with pointed tips. Perine disintegrates very easily on acetolysis.

11. *Nephrolepis biserrata* (Damansara Road, Kuala Lumpur, Selangor; Khoo Eng Ee KLU 12305; Plate 7, Figs. 3–4).

Spores monolete-bilateral, 25–30 × 33–40 × 23–29 μ. Amb oblong. Proximal face flat to slightly concave; distal face convex. Laesura 20 μ, margins thickened into lips of 1 μ broad, tapering towards the tips. Exine 2 μ thick, sexine thicker than nexine, verrucose to tuberculose; verrucae 1 μ high and 4–6 μ broad. Perine thin, more or less verrucose and easily disintegrates on acetolysis.

PTERIDIOIDEAE

12. *Histiopteris stipulacea* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12306; Plate 7, Figs. 1–2).

Spores monolete-bilateral, 38–48 × 59–65 × 43–46 μ. Amb oblong. Proximal face slightly concave; distal face convex. Laesura 40 μ, margins thickened slightly into lips of 6–10 μ broad and tapering towards the tips. Exine 5 μ thick, sexine thicker than nexine, densely verrucose-tuberculose; verrucae or tubercles granulose, 5 μ high, 6 μ broad, and 8–22 μ long. Perine absent.

13. *Pteris vittata* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12306; Plate 1, Figs. 1–3).

Spores trilete-tetrahedral, 48–53 × 61–65 μ. Amb triangular with nearly straight sides and rounded corners. Proximal face flat to slightly convex; distal face hemispherical. Laesura 27 μ, margins thickened into lips of 3 μ broad and tapering towards the tips. Exine 3 μ thick, sexine much thicker than nexine, densely rugulose; rugulae up to 6 μ tall, sometimes coalescing to form a coarse reticulum. On the proximal face there are 3 ridges parallel and close to the laesura arms. Equator collar present; this is a collar-like ridge which protrudes as a flange around the spores, separating the proximal and the distal parts of the spores, up to 7 μ high, often interrupted. Perine absent.

14. *Acrostichum aureum* (Lukut, Negeri Sembilan; Turnau KLU 2925; Plate 2, Fig. 1).

Spores trilete-tetrahedral, 42–49 × 50–60 μ. Amb rounded triangular with slightly convex sides and broadly rounded corners. Proximal face conical with straight sides and angular pole; distal face hemispherical. Laesura 21 μ, margins thickened into lips of 1 μ broad and tapering towards the tips. Exine 2 μ thick, sexine thicker than nexine, granulose. Perine not seen.

15. *Stenochlaena palustris* (Damansara Road, Kuala Lumpur, Selangor; Khoo Eng Ee KLU 12311; Plate 7, Figs. 5–6).

Spores monolete-bilateral, 30–37 × 39–53 × 30–36 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 29 μ, margins thickened into lips of 1 μ broad. Exine 3 μ thick, sexine thicker than nexine, provided with conical tubercles of 2 μ tall with rounded tips and base diameter of 2 μ. Perine absent.

ASPLENIOIDEAE

16. *Asplenium nidus* var. *musifolia* (Damansara Road, Kuala Lumpur; Khoo Eng Ee KLU 12304; Plate 3, Figs. 1–2).

Spores monolete-bilateral, 27–36 × 30–50 × 27–32 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 20 μ, margins thickened slightly into lips of 3 μ broad. Exine 1 μ thick, sexine as thick as nexine, smooth. Perine finely granulose, wrinkled into discontinous, closely sinuous folds protruding up to 3 μ from the exine surface, with smooth crests.

BLECHNOIDEAE

17. *Blechnum orientale* (Ulu Gombak Road, Selangor; Khoo Eng Ee KLU 12308; Plate 3, Figs. 3–4).

Spores monolete-bilateral, 34–39 × 44–51 × 36–46 μ. Amb oblong. Proximal face flat; distal face hemispherical. Laesura 29 μ, margins thickened into lips 3 μ broad and tapering towards the tips. Exine 1 μ thick, sexine as thick as nexine, smooth. Perine sparsely granulose, loosely folded into sparse, thin indistinct folds protruding up to 3 μ from the exine surface, with smooth crests; disintegrates easily on acetolysis.

18. *Brainea insignis* (Tanjong Selantai, Johore; Abd. Samat b. Abdullah KLU 1869; Plate 10, Figs. 4–6).

Spores monolete-bilateral, 31–42 × 35–50 × 29 43 μ. Amb oblong to subspherical. Proximal face slightly convex; distal face hemispherical. Laesura 27 μ, margins thickened into lips of 1 μ thick and tapering towards the tips. Exine 2 μ thick, sexine as thick as nexine, smooth. Perine densely granulose, closely adherent to the exine nearly without folds or only with one or two indistinct short folds which protrude up to 2 μ from the exine surface; disintegrates easily on acetolysis.

LOMARIOPSIDOIDEAE

19. *Egenolfia appendiculata* (Kuah, Langkawi, Kedah; Abd. Samat b. Abdullah KLU 2316; Plate 10, Fig. 3).

Spores monolete-bilateral, 32–36 × 31–39 × 26–37 μ. Amb subspherical to circular in outline. Proximal face flat to slightly convex; distal face hemispherical. Laesura 19 μ, slightly thickened into lips of 1 μ broad; in some spores forked in one end. Exine 1 μ thick, sexine as thick as nexine, smooth. Perine with finely reticulate patterns, loose, lightly folded into very many elongated sharp ridges most of which radiate from the centre to the periphery of the spores and protruding up to 7 μ from the exine surface; disintegrates on acetolysis.

20. *Bolbitis heteroclita* (Jengka Forest Reserve, Pahang; Turnau KLU 2894; Plate 10, Figs. 1–2).

Spores monolete-bilateral, 31–37 × 35–42 × 35–38 μ. Amb oblong to subspherical. Proximal face flat to convex; distal face hemispherical. Laesura 21 μ, margins slightly thickened into smooth lips of 1 μ broad. Exine 1 μ thick, sexine as thick as nexine, smooth. Perine sparcely covered with minute spinules, highly folded into sinuous and elongated ridges radiating from the centre to the periphery of the spores; folds protrude up to 12 μ from the exine surface, with undulating crests; disintegrates on acetolysis.

21. *Teratophyllum aculeatum* var. *montanum* (Tringkap, Pahang Abd. Samat b. Abdullah KLU 2288; Plate 5, Figs. 1–3).

Spores monolete-bilateral, 47–60 × 66–71 μ (polar view not obtained). Proximal face convex to hemispherical; distal face hemispherical. Laesura 27–30 μ. Exine very thin, less than 1 μ thick, not subdivided into distinct sexine and nexine. Perine densely crowded with minute spinules less than 1 μ high, very sparsely folded into faint folds which protrude up to 19 μ from the exine surface; with smooth crests; cracked up on acetolysis.

22. *Lomagramma sumatrana* (22nd mile Bentong Road, Selangor; Turnau KLU 2914; Plate 9, Figs. 1–2).

Spores monolete-bilateral, 31–43 × 50–58 × 35–40 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 29 μ, margins slightly thickened into lips of 1 μ broad. Exine 2 μ thick, sexine slightly thinner than nexine, finely granulose to spinulose. Perine absent.

23. *Elaphoglossum callifolium* (Tanah Rata, Pahang; Mahmud b. Sider KLU 4612; Plate 4, Figs. 1–2).

Spores monolete-bilateral, 18–30 × 23–40 × 18–22 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 18 μ. Exine 1 μ thick, sexine and nexine are not clearly differentiated, smooth. Perine minutely spinulose, sparsely folded into thin, sharp sinuous ridges protruding up to 7 μ from the exine surface; disintegrates on acetolysis.

DRYOPTERIDOIDEAE

24. *Dryopteris sparsa* (Maxwell Hills, Perak; Evans KLU 2493; Plate 3, Figs. 5–6).

Spores monolete-bilateral, 22–27 × 38–46 × 28–31 μ. Amb oblong. Proximal face flat to slightly concave; distal face convex. Laesura 20 μ, margins thickened very slightly into lips of 1 μ broad. Exine 1 μ thick, sexine as thick as nexine, smooth. Perine smooth, fairly closely adherent to the exine, folded into lobate crowded ridges protruding up to 11 μ from the exine surface; with many undulating crests; disintegrates on acetolysis.

TECTARIOIDEAE

25. *Arcypteris irregularis* (Ulu Gombak Road, Selangor; Wee & Lim KLU 1975; Plate 5, Figs. 4–6).

Spores monolete-bilateral, 20–29 × 32–39 × 23–26 μ. Amb oblong. Proximal face flat; distal face hemispherical. Laesura 20 μ, margins faintly thickened into lips of 1 μ broad. Exine 1.5 μ thick, sexine as thick as nexine, smooth. Perine with very minute spinules, folded into a few elongated sharp, thin ridges radiating from the centre to the periphery of the spores; folds protrude up to 10 μ from the exine surface; disintegrates easily on acetolysis.

26. *Heterogonium pinnatum* (Templer Park, Selangor; Abd. Samat b. Abdullah KLU 2636; Plate 4, Figs. 3–4).

Spores monolete-bilateral, 28–40 × 40–50 × 33–36 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 27 μ, margins faintly thickened into lips of 1 μ broad. Exine 2 μ thick, sexine as thick as nexine, smooth, breaking up on acetolysis. Perine minutely spinulose (spines less than 1 μ tall), highly folded up into elongated, closely sinuous ridges protruding up to 6 μ from the exine surface; disintegrates on acetolysis.

ATHYRIOIDEAE

27. *Athyrium pinnatum* (Genting Simpah, Selangor; Turnau KLU 2785; Plate 9, Figs. 5–6).

Spores monolete-bilateral, 20–27 × 33–44 × 24–25 μ. Amb oblong. Proximal face flat to convex; distal face hemispherical. Laesura 23 μ, margins faintly thickened into lips of 1 μ broad. Exine 2 μ thick, sexine as thick as nexine, smooth. Perine faintly granulose, closely adherent to the exine, with a few folds; folds appear as irregular ridges protruding up to 2 μ from the exine surface; disintegrates on acetolysis.

28. *Cystopteris tenuisecta* (Cameron Highlands, Pahang; Poore KLU 256; Plate 8, Figs 1–3).

Spores monolete-bilateral, 30–45 × 45–60 × 31–45 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 30 μ, margins slightly thickened into lips of 1 μ broad. Exine 2 μ thick, sexine thicker than nexine, densely finely spinulose. Perine folded; folds anastomose to form dense reticulum, provided with numerous rod-like protuberances about 3–4 μ high; tips of rods peltately lobed.

Discussion

Spore morphology of 28 Malaysian species included by Holttum (1954) in the Dennstaedtiaceae shows a great diversity of form, size and structure. Based on whether the spores are monolete-bilateral or trilete-tetrahedral, with or without perine, and perine if present smooth or variously patterned, etc., there seem to be at least seven distinct types of spores. These spore-types are:

Type-1: Spore trilete-tetrahedral, provided with well-developed equatorial collar (*Pteris vittata*).

Type-2: Spore trilete-tetrahedral, without equatorial collar, without or occasionally with a thin spinulose perine (*Acrostichum aureum, Isoloma divergens, Lindsaea scandens, Microlepia speluncae,* and *Orthiopteris kingii*).

Type-3: Spore monolete-bilateral, provided with folded or reticulate perine, plano-convex or concave-convex in equatorial view (*Asplinium nidus* var. *musifolia, Blechnum orientale, Dryopteris sparsa, Elaphoglossum callifolium, Heterogonium pinnatum, Oleandra pistillaris, Arcypteris irregularis,* and *Teratophyllum aculeatum*).

Type-4: Spore monolete-bilateral, without or occasionally with very thin perine, exine provided with low, flattish, roundish or conical protuberances (*Davallia divaricata, Histiopteris stipulacea, Humata heterophylla, Nephrolepis biserrata,* and *Stenochlaena palustris*).

Type-5: Spore monolete-bilateral, plano-convex, perine provided with spine-like or rod-like blunt processes (*Cystopteris tenuisecta, Hypolepis bivalvis*).

Type-6: Spore monolete-bilateral, concave-convex or plano-convex, with or without perine; perine if present thin, hardly folded and easily dissolved on acetolysis (*Athyrium pinnatum, Lomagramma sumatrana, Sphenomeris chusana,* and *Tapeinidium pinnatum*).

Type-7: Spore monolete-bilateral, biconvex or sometimes plano-convex, provided with folded, reticulate or finely patterned perine (*Bolbitis heteroclita, Brainea insignis,* and *Egenolfia appendiculata*).

In the Dennstaedtioideae, Holttum included *Dennstaedtia, Hypolepis, Microlepia* and *Orthiopteris. Hypolepis* with a monolete-bilateral spore of type-5 seems to be out of place in this subfamily, since the other three genera have trilete-tetrahedral spores of type-2. Furthermore, the perine in *Hypolepis* is provided with spine-like or rod-like minute processes, while the perine of *Dennstaedtia* and *Orthiopteris,* if present, is not so patterned, and in *Microlepia* the spores are without perine. Erdtman & Sorsa (1971) included these four genera in the family Pteridaceae in which 52 out of 65 genera have exclusively trilete-tetrahedral spores, 7 possess mainly trilete but occasionally also monolete spores, and 6 genera with exclusively monolete-bilateral spores. Apart from *Hypolepis,* the other five genera which have exclusively monolete-bilateral spores are:— *Humblotiella, Tapeinidium, Sphenomeris, Paesia,* and *Lonchitis.* Perine of these genera, if present, is very thin, hardly folded and is easily detached from the exine on acetolysis, unlike that of *Hypolepis.* In Holttum's classification, *Tapeinidium* and *Sphenomeris,* on the other hand, were grouped together with *Lindsaea, Schizoloma* and *Isoloma* in the Lindsaeoideae. Spore morphology does not support this grouping, since both *Isoloma* and *Lindsaea* have a trilete-tetrahedral spore of type-2, whereas *Sphenomeris* and *Tapeinidium* have a monolete-bilateral spore of type-6.

Of the Davallioideae, the four genera (i.e. *Araiostegia, Davallia, Humata,* and *Leucostegia*) assigned by Holttum (1954) in this subfamily have a more or less similar spore-type, namely monolete-bilateral, without perine, and the exine is provided with low flattish verrucae or tubercles (spore type-4). For these features, the spores of *Nephrolepis, Histiopteris* and *Stenochlaena* agree very well. Holttum (1954), on the other hand, placed *Nephrolepis* together with *Oleandra* in the Oleandroideae. Spores of *Oleandra* are, however, different from those of *Nephrolepis* by being provided with folded perine, the detailed structure of which matches very well with that of *Elaphoglossum, Arcypteris,* and *Teratophyllum* (spore type-3). *Histiopteris* and *Stenochlaena* together with *Acrostichum, Pteridium* and *Pteris* were included by Holttum (l.c.) in the Pteridioideae. *Acrostichum* and *Pteridium* possess a trilete-tetrahedral spores of type-2, whereas *Pteris* has spores of type-1.

The genus *Asplenium* (included by Holttum in the Asplenioideae) has spores which are very much similar to those of *Blechnum* and *Heterogonium* (spore type-3). However, *Blechnum* was assigned by Holttum in the Blechnoideae together with *Brainea* and *Woodwardia.* While spores of *Woodwardia* match very well with those of *Blechnum,* that of *Brainea* being monolete-bilateral, biconvex and provided with folded, granulose-reticulose perine, agree well with the spores of *Bolbitis* and *Egenolfia* (spore type-7). The last two mentioned genera were placed together with *Elaphoglossum, Lomagramma, Lomariopsis* and *Teratophyllum* in the Lomariopsidoideae by Holttum. While spores of *Elaphoglossum* and *Teratophyllum* are very much similar to that of *Oleandra* and *Tectaria* (spore type-3), those of *Lomagramma,* being without perine, agree well with the spores of *Athyrium, Sphenomeris* and *Tapeinidium* (spore type-6). According to Erdtman & Sorsa (1971), some species of *Lomariopsis* possess perinous spores similar to those described as type-3, while others have a spore of type-6.

In the Dryopteridoideae, Holttum assigned *Acrophorus, Diacalpe, Didymochlaena, Dryopteris, Polystichum* and *Polystichopsis.* These genera have more or less uniform spores which match very well with those of *Asplenium, Blechnum* and *Heterogonium* (Spore type-3). Similarly, the spores of ten genera included by Holttum in the Tectarioideae (*Arcypteris, Ctenitis, Cyclopeltis, Heterogonium, Hypodematium, Lastreopsis, Pleocnemia, Pteridrys, Quercifilix* and *Tectaria*) agree well with each other and more or less similar to those of spore type-3.

Of the Athyroideae, Holttum place two Malaysian genera, namely *Athyrium* and *Cystopteris.* As has been indicated above, the spores of *Athyrium* belong to spore type-3, whereas those of *Cystopteris* to spore type-5.

The above discussion seems to indicate that apart from the Davallioideae, Dryopteridoideae and Tectarioideae, the other subfamilies of the Dennstaedtiaceae as defined by Holttum, show very diverse types of spores and that spore morphology does not lend any support to the disposition of various genera either in the different subfamilies as recognised by Holttum (1954) or in the various families as subscribed by Copeland (1947), Reimers (1954), Pichi Sermolli (1958) and others.

However, this does not imply that the classification of the genera included by Holttum in the Dennstaedtiaceae should match well with the spore types, but rather that it demonstrates that more palynological studies, especially on those of the tropical taxa should be done, so that morphological characters of the spores could be considered along with other attributes in constructing a more natural system of classification.

Finally, it should be emphasised here that, since the number of species of which the spores have been studied in detail, is very small, and that, it is also well known that even within a single genus the spore morphology may vary considerably, the above findings should be considered with great caution.

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References

Atkinson, L. R., 1973. The gametophyte and family relationships. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns.* 73–90.

Ching, R. C., 1940. On natural classification of the family Polypodiaceae. *Sunyatsenia* 5, 201–268.

Christensen, C., 1938. Filicinae. In F. Verdoorn (Ed.) — *Manual of Pteridology.* 522–550.

Copeland, E. B., 1947. *Genera Filicum.* Chronica Botanica. Waltham Mass., U.S.A.

Erdtman, G., 1957. *Pollen and Spore Morphology/Plant Taxonomy* — II. — Gymnospermae, Pteridophyta, Bryophyta.

——————— & P. Sorsa, 1971. *Pollen and Spore Morphology/Plant Taxonomy — IV. —* Pteridophyta.

Harris, W. F., 1955. *A manual of the spores of New Zealand Pteridophyta.* N.Z. Dept. Sci. Industr. Res. Bull. 116, 186 pp. Willington.

Holttum, R. E. 1947. A revised classification of Leptosporangiate ferns. *J. Linn. Soc. (Bot.) Lond.* **52**, 123–158.

——————— 1949. The classification of ferns. *Biol. Rev.* **24**, 267–295.

——————— 1954. A Revised Flora of Malaya — II. *Ferns of Malaya,* 299–574. Govt. Printing Office Singapore.

——————— 1973. Introduction to Pteridophyta. In J. C. Willis (Revised by H. K. Airy Shaw) *Dict. Fl. Pl. & Ferns.* 8th. edition. Cambridge University Press.

Lovis, J. D., 1973. A biosystematic approach to phylogenetic problems and its application to the Aspleniaceae. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns,* 211–227.

Manton, I., 1961. Evolution in the Pteridophyta. In P. J. Wanstall (Ed.) — *A Darwin Centenary Bot. Soc. Brit. Isle Conf. Rep.* **6**, 105–119

Mickel, J. T., 1973. The classification and phylogenetic position of the Dennstaedtiaceae. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns,* 135–144.

Nayar, B. K., 1970. A phylogenetic classification of the homosporous ferns. *Taxon* **19**, 229–236.

Nayar, B. K. & S. Devi, 1963. Spore morphology of some Japanese Aspidiaceae. *Pollen Spores* **5**, 354–372.

——————— 1964 a. Spore morphology of Indian ferns-I. Aspidiaceae. *Grana Palynol.* **5**, 80–120.

——————— 1964 b. Spore morphology of Indian ferns-II Aspleniaceae & Blechnaceae. *Grana Palynol.* **5**, 222–242.

——————— 1966. Spore morphology of the Pteridaceae-I. The Pteridoid ferns *Grana Palynol.* **6**, 476–497.

——————— 1967. Spore morphology of the Pteridaceae — II. The Gymnogrammoid ferns. *Grana Palynol.* **7**, 568–600.

——————— 1968a. Spore morphology of the Pteridaceae. III. The Dicksonioid, Dennstaedtioid and Lindsayoid ferns. *Grana Palynol.* **8**, 185–203.

——————— 1968b. Spore morphology of the Pteridaceae. IV. Taxonomic and phyletic considerations. *Grana Palynol.* **8**, 517–535.

Nayar B. K. & S. Kaur, 1963. Spore morphology of some Indian members of the Lomariopsidaceae. *Pollen Spores* **5**, 87–94.

Pichi Sermolli, R. E. G., 1958. The higher taxa of the Pteridophyta and their classification. *Uppsala Univ. Arsskrift.,* **6**, 70–90.

——————— 1973. Historical review of the higher classification of the Filicopsida. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns,* 11–40

Reimers, H., 1954. Pteridophyta. Farnpflanzen. In *Engler's Syllabus der Pflanzenfamilien, 12 Aufl.* **I**, 269–311. Berlin.

Sen, U. & T. Sen, 1973. Anatomical relationships between the *Oleandra* and *Nephrolepis* groups. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns,* 155–172.

Sledge, W. A., 1973. Generic and family boundaries in the Aspidiaceae and Athyriaceae. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns,* 203–210.

Swain, T. & G. Cooper-Driver, 1973. Biochemical systematics in the Filicopsida. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns,* 111–134.

Tardieu-Blot, M. L., 1963a. Sur les spores de Lindsaeaceae et de Dennstaedtiaceae de Madagascar et des Mascareignes, étude de palynologie appliquée a la systematique. *Pollen Spores* **5**, 69–86.

——————— 1963b. Sur les spores de Pterideae Malgaches. *Pollen Spores* **5**, 337–353.

——————— 1965. Sur les spores d'Adiantaceae, Aspleniaceae, Thelypteridaceae et Athyriaceae de Madagascar. *Pollen Spores* **7**, 319–338.

Van Cotthem, W. R. J., 1973. Stomatal types and systematics. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns,* 59–71.

Walker, T. G., 1973. Evidence from cytology in the classification of ferns. In A. C. Jermy *et al* (Ed.) — *The phylogeny and classification of the ferns,* 91–110.

Willis, J. C., 1973. *Dict. Fl. Pl. & Ferns.* (Revised by H. K. Airy Shaw). 8th ed. Cambridge Univ. Press.

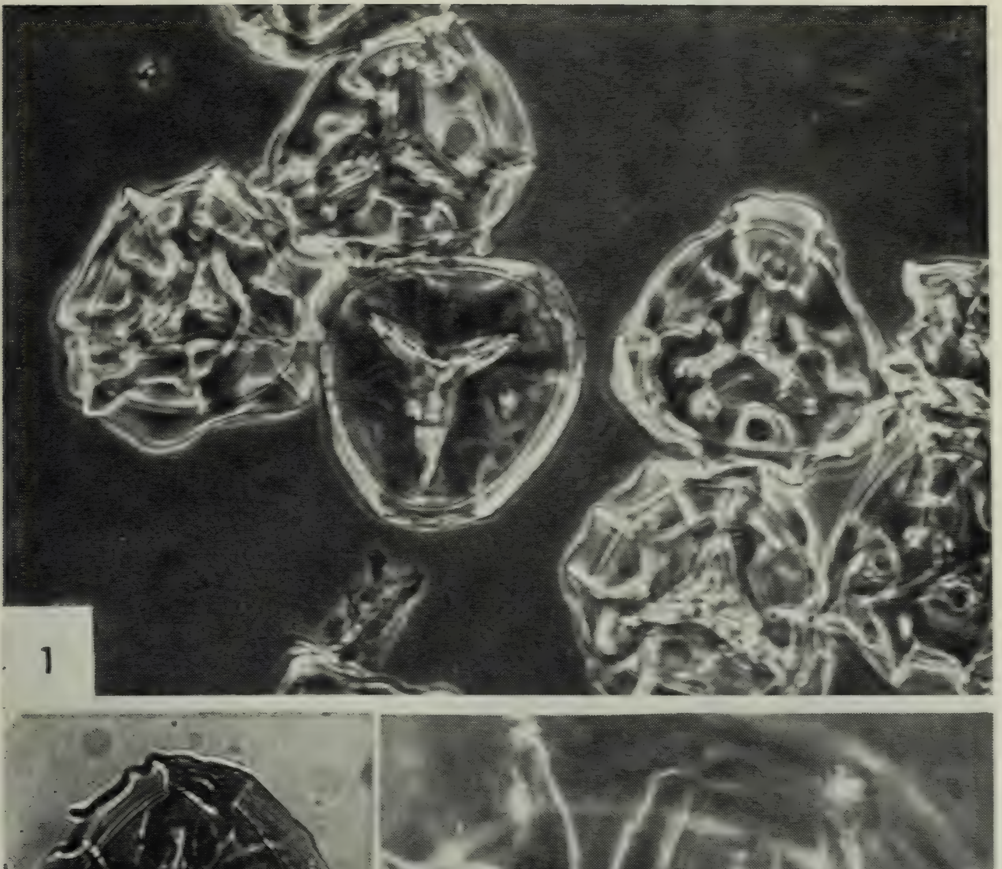

Plate 1. Figs. 1–3: *Pteris vittata;* 1 — pr.p.v. spore in the centre is in optical section: 2 — obl.e.v.; 3 — detailed structure of distal polar wall of perine layer.
(abbrev. in legends: **pr.p.v.** = proximal polar view, **obl.e.v.** = oblique equatorial view, **d** = distal)

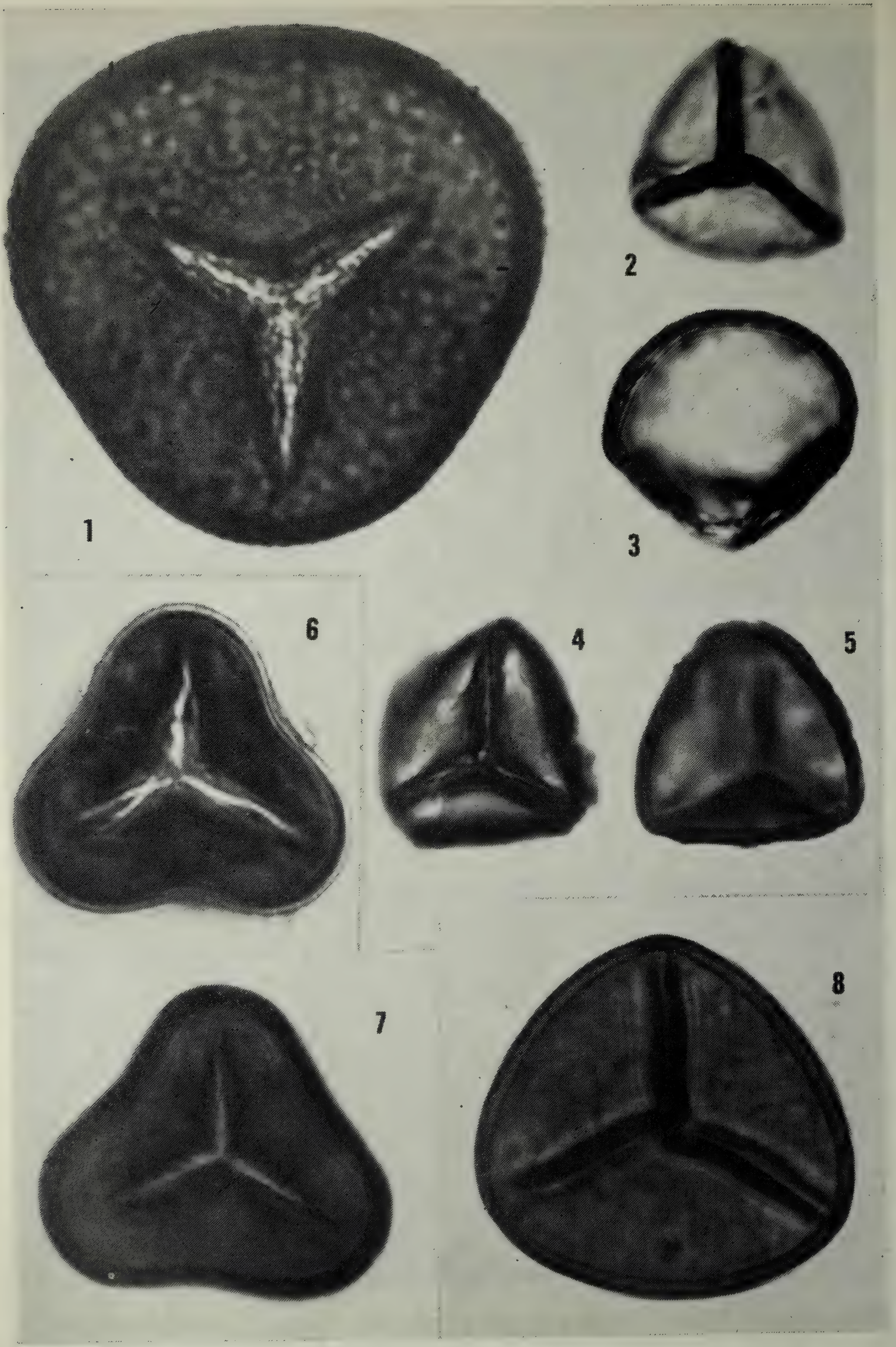

Plate 2. Fig. 1 — *Acrostichum aureum,* pr.p.v.; figs. 2 & 3 — *Lindsaea scandens,* pr.p.v. & e.v. respectively; figs. 4 & 5: *Isoloma divergens,* 4 — pr.p.v., 5 — optical section of 4; fis. 6 & 7: *Microlepia speluncae,* 6 — pr.p.v., 7 — optical section of 6; fig. 8 — *Orthiopteris kingii,* optical section of pr.p.v.

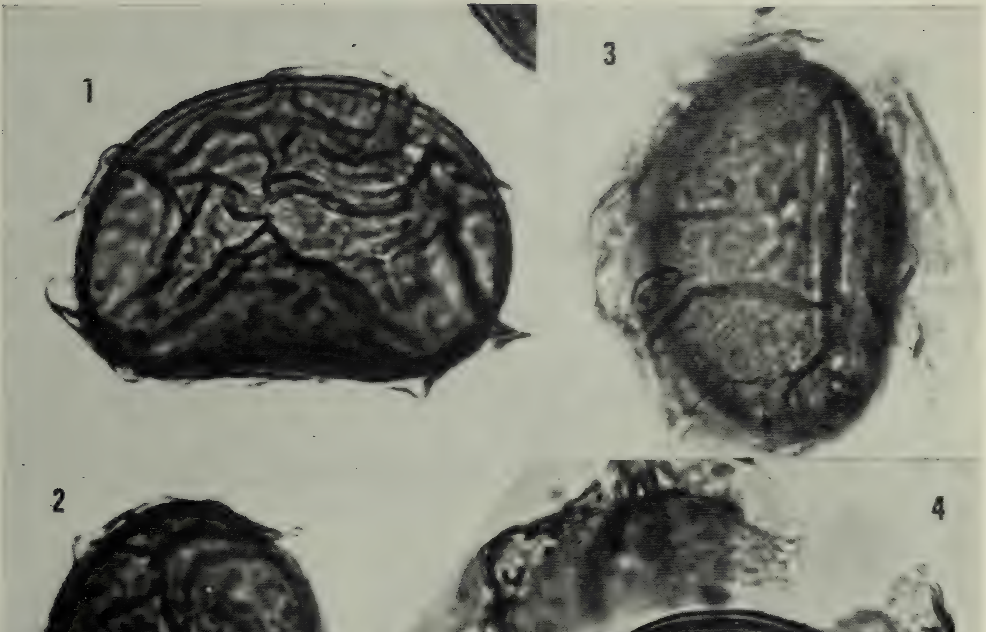

Plate 3. Figs. 1 & 2: *Asplenium nidus* var. *musifolia,* 1 — e.v., 2 — pr.p.v.; figs. 3 & 4: *Blechnum orientale,* 3 — obl.pr.p.v., 4 — e.v. with broken perine; figs. 5 & 6: *Dryopteris sparsa,* 5 — obl.pr.p.v., 6 — e.v.

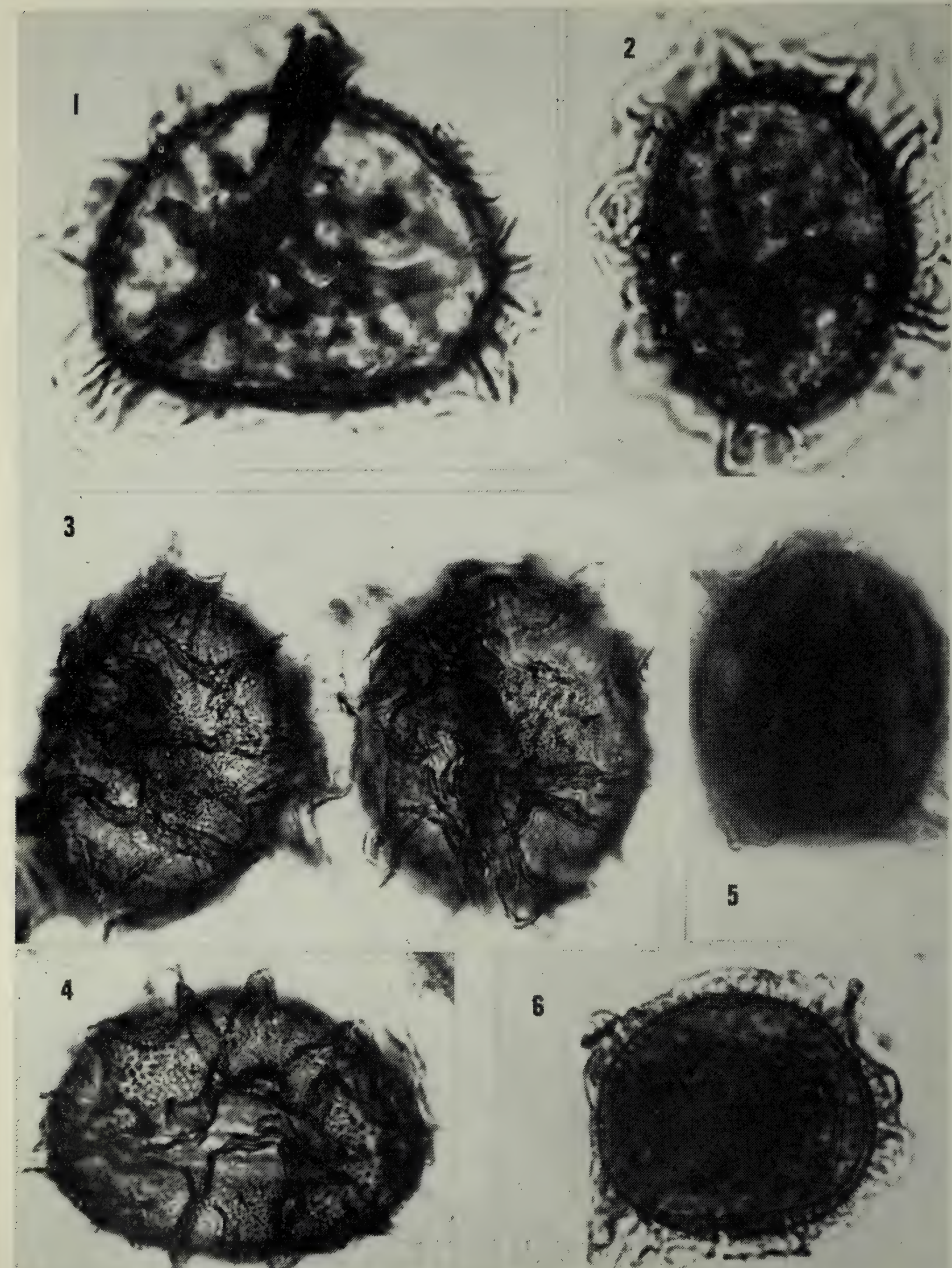

Plate 4. Figs. 1–2: *Elaphoglossum callifolium*, 1 — e.v., 2 — d.p.v.; figs. 3 & 4: *Heterogonium pinnatum*, 3 — *left*, e.v., *right*, d.p.v., 4 — pr.p.v.; figs. 5 & 6: *Oleandra pistillaris*, d.p.v., 5 — focus on perine, 6 — optical section.

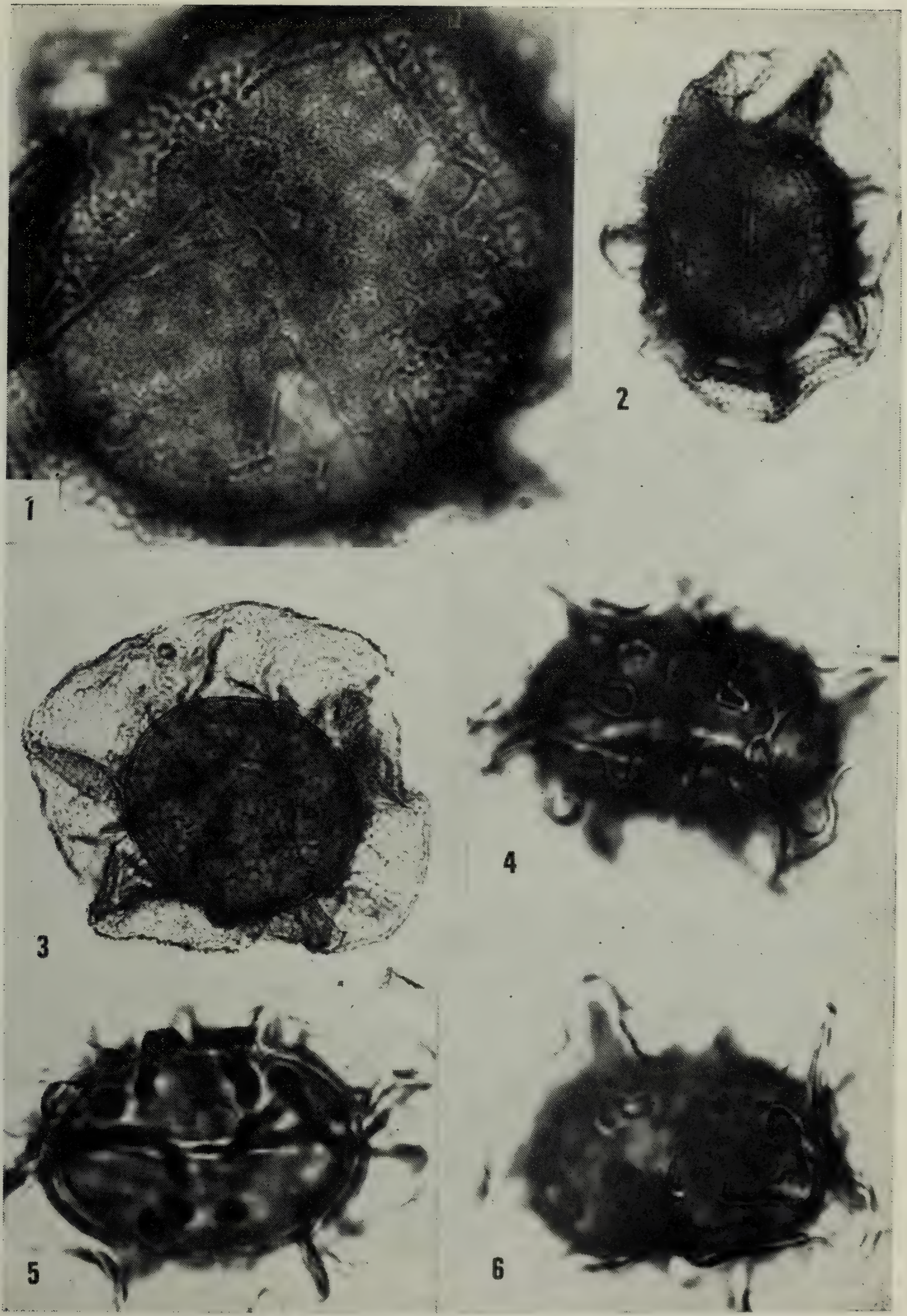

Plate 5. Figs. 1–3: *Teratophyllum aculeatum* var. *montanum*, 1 — d.p.v. showing detailed structure of perine, 2 — pr.p.v., 3 — obl.e.v.; figs. 4–6: *Arcypteris irregularis*, 4 — obl.pr.p.v., 5 — pr.p.v. in optical section, 6 — d.p.v.

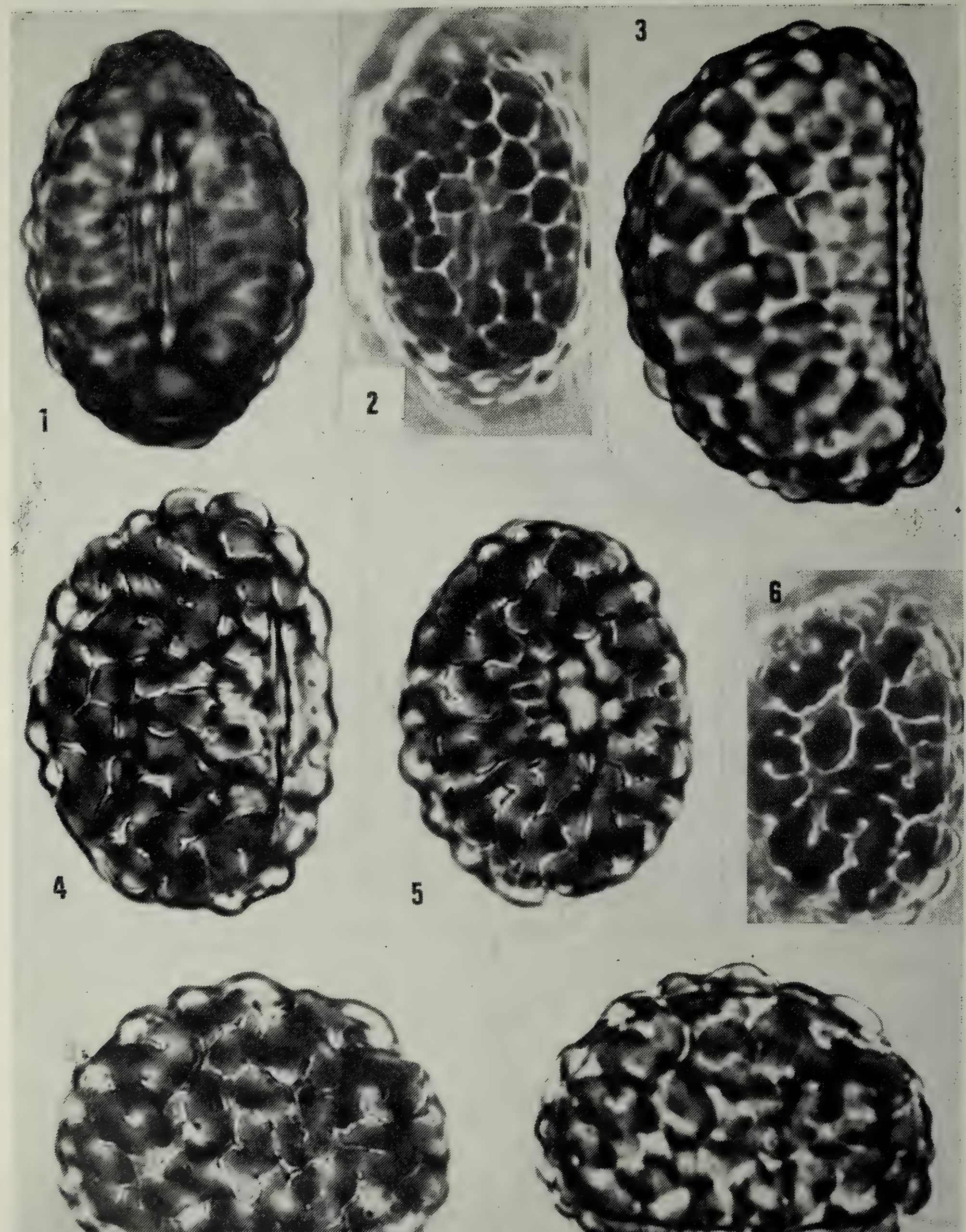

Plate 6. Figs. 1–3: *Davallia divaricata,* 1 — pr.p.v. in optical section, 2 — detailed structure of exine in pr.p.v., 3 — e.v. in optical section; figs. 4–8: *Humata heterophylla,* 4 — obl.e.v., 5 — pr.p.v., 6 — d.p.v., 7 — e.v., 8 — e.v. in optical section.

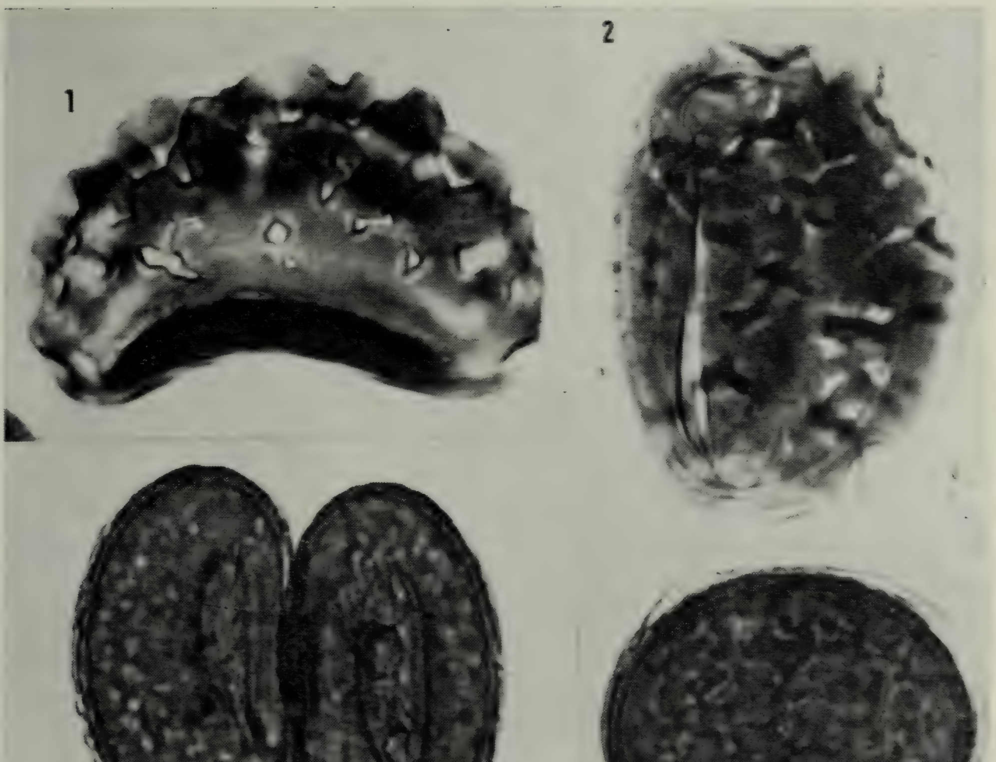

Plate 7. Figs. 1 & 2: *Histiopteris stipulacea*, 1 — e.v., 2 — obl.pr.p.v.; figs. 3 & 4 *Nephrolepis biserrata*, 3 — pr.p.v., 4 — e.v.; 5 & 6: *Stenochlaena palustris*, 5 — pr.p.v. in optical section, 6 — e.v. in optical section.

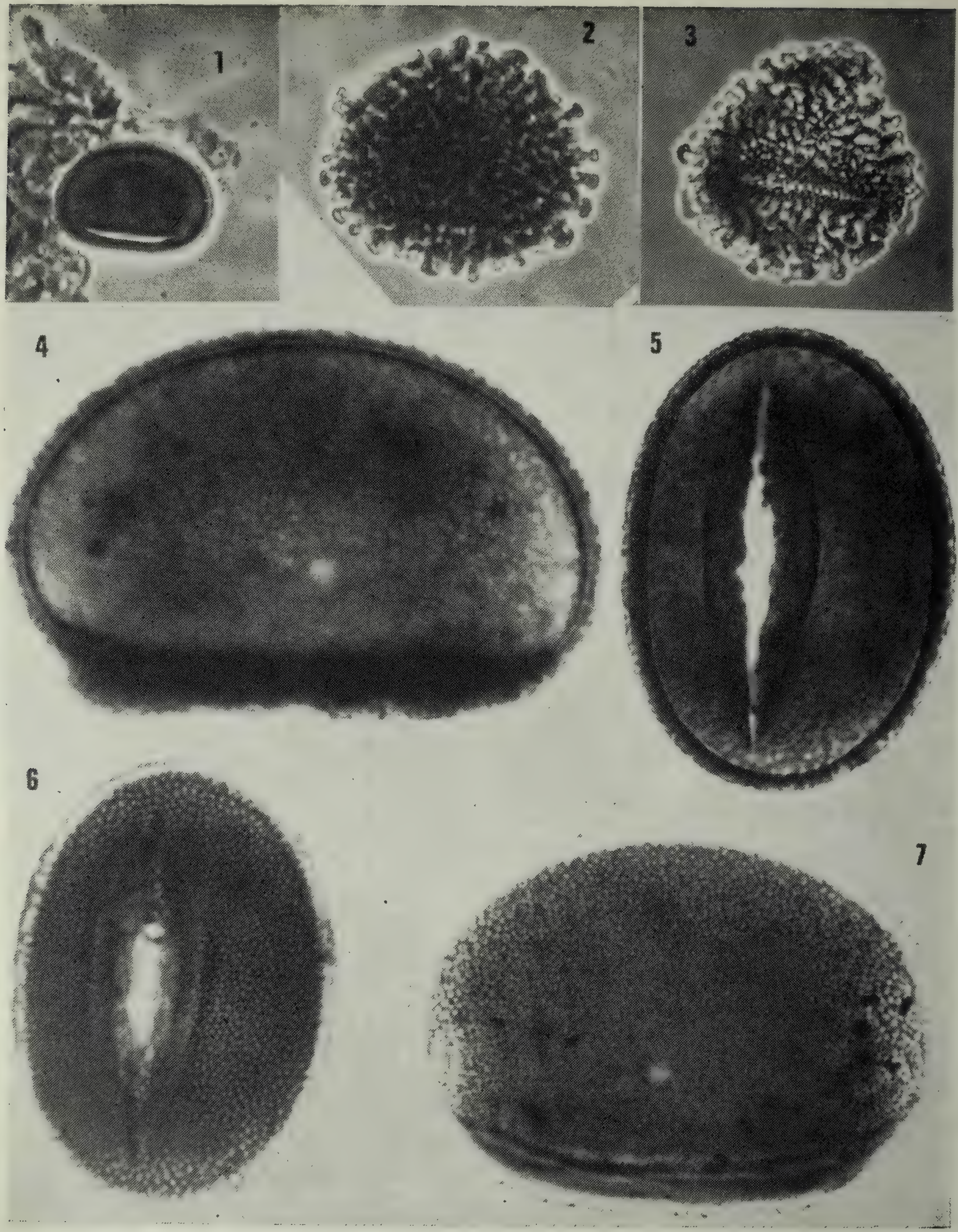

Plate 8. Figs. 1–3: *Cystopteris tenuisecta*, 1 — obl.e.v. with ruptured perine, 2 — d.p.v., 3 — pr.p.v.; figs. 4–7: *Hypolepis bivalvis*, 4 — e.v. in optical section, 5 — pr. p.v. in optical section, 6 — pr.p.v., 7 — e.v.

Plate 9. Figs. 1–2: *Lomagramma sumatrana,* 1 — e.v., 2 — obl.pr.p.v.; fig. 3 — *Sphenomeris chusana,* obl.e.v.; fig. 4 — *Tapeinidium pinnatum,* obl.e.v.; figs. 5 & 6: *Athyrium pinnatum,* 5 — obl.pr.p.v., 6 — e.v.

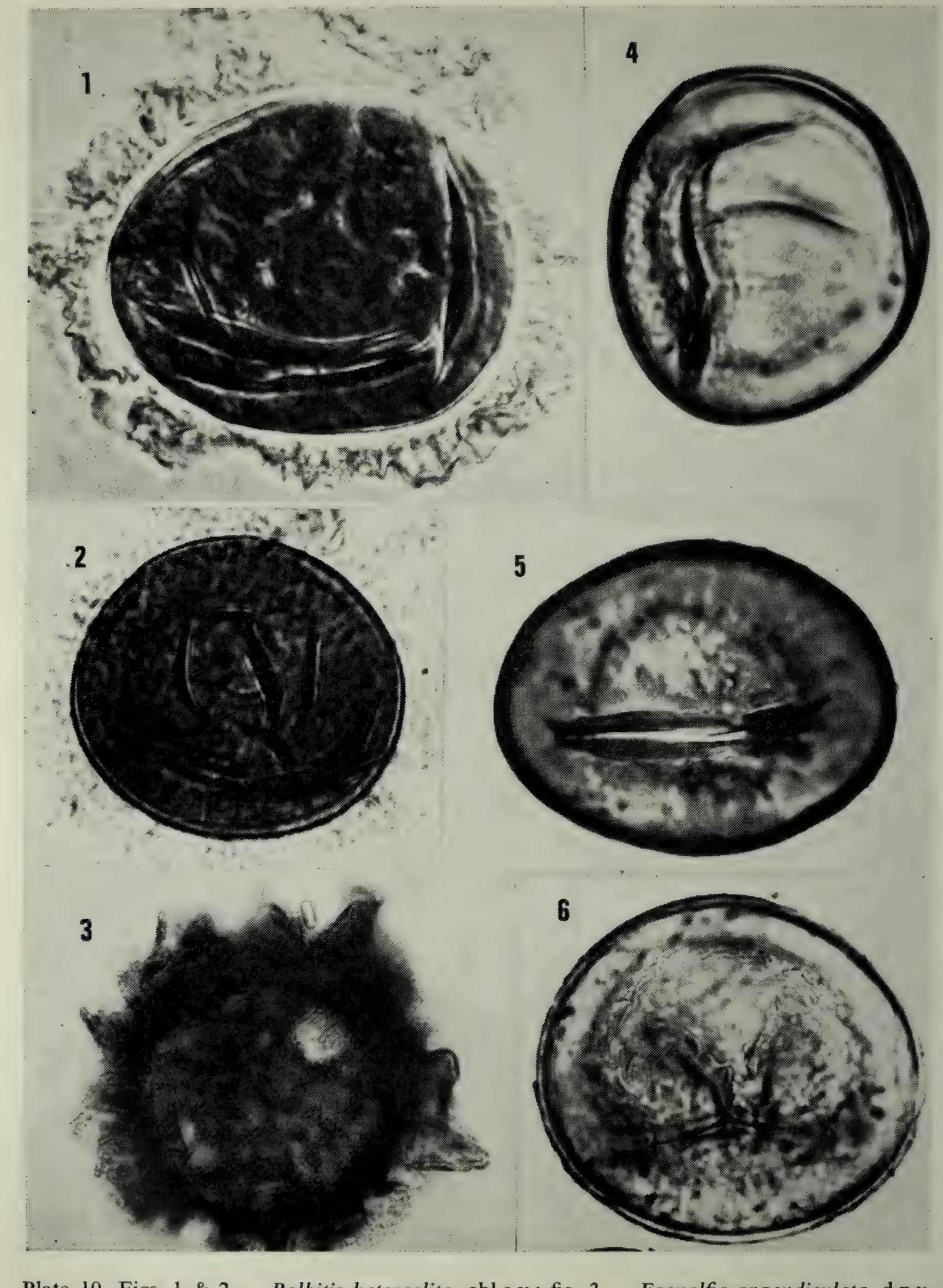

Plate 10. Figs. 1 & 2 — *Bolbitis heteroclita,* obl.e.v.; fig. 3 — *Egenolfia appendiculata,* d.p.v., figs. 4–6: *Brainea insignis,* 4— obl.e.v., 5 — pr.p.v. in optical section, 6 — d.p.v.

An Enumeration of the Malesian Species of Aralia L.

by

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The species of *Aralia* in South-east Asia and the adjacent islands have been subject to considerable misunderstanding. The present account takes a broad view of specific limits, following along lines originally proposed by van Steenis (Bull. Bot. Gard. Buitenz. ser. 3, 17 (1948) 391).

Aralia

Linn. Sp. Pl. (1753) 273. — *Acanthophora* Merr. Philip. J. Sc. 13 (1918) 316; Steen. Bull. Bot. Gard. Btzg. ser 3, 17 (1948) 390.

Sparingly branched shrubs or small trees, or climbing, rarely (extra Malesia) herbaceous, glabrous or hairy, often prickly. Leaves pinnate to tri-pinnate, usually with leaflets at the insertion of the lateral pinnae; leaflets serrate; petiole with a sheathing base. Inflorescence a terminal panicle; flowers sessile or pedicellate, with an articulation below the flower; calyx with 5–6 teeth; petals 5–6, imbricate; ovary 2–6 celled; styles 2–6 free or shortly connate below. Fruit a fleshy drupe; pyrenes cartilaginous compressed; endosperm uniform.

DISTR. More than 30 species in North America and Asia. In Malesia 6 species, extending from Sumatra and the Malay Peninsula through Borneo and Celebes to the Philippines and West New Guinea.

ECOL. Usually on scrubby hillsides and in second growth, often in ravines or near streams, or in thickets near or above the limit of tree-growth. Occurring at low altitudes (100 m) but usually in the montane zone, up to 3000 m.

Notes. Hui-Lin Li in Sargentia 2 (1942) 101, treats some species that extend into Malesia. Merrill considered that the climbing habit and recurved spines of *Acanthophora* justified its separation as a distinct genus, but more recent authors have not agreed.

KEY TO THE SPECIES

1. a. Flowers sessile (capitate) or very shortly pedicellate 2
   b. Flowers pedicellate (umbellate) 3
2. a. Flowers sessile, underside of leaf ± densely tomentose, hairs of the branches and inflorescence ± appressed and felted, bracts around the capitula enveloped in hairs .... 1. *A. dasyphylla*
   b. Flowers short pedicellate, underside of leaf sparsely tomentose, hairs of the branches and inflorescence ± patent, bracts around the capitula less densely tomentose .... 2. *A. javanica*
3. a. Climbing or scrambling liane, spines curved .... 3. *A. scandens*
   b. Erect shrubs or small trees, spines straight 4

4\. a. Leaflets glaucous beneath, margins with few crenations, fruit small (± 3 mm long) .... 4. *A. bipinnata*

b. Leaflets green (or with fawn pubescence) beneath, margins serrate, fruit rather larger (4–6 mm long) 5

5\. a. Young parts and under-surface of leaves glabrous (but with small spines) .... 5. *A. ferox*

b. Young parts and under-surface of leaves pubescent .... 6. *A. montana*

1\. *Aralia dasyphylla* Miq. Fl. Ind. Bat. 1, 1 (1856) 751. — *A. urticifolia* Bl. ex Miq. Ann. Mus. Bot. Lugd. -Bat. 1 (1863). — *A. dasyphylla* var. *strigosa* Miq. Ann. Mus. Bot. -Lugd. — Bat. 1 (1863) 9. — *A. dasyphylla* var. *latifolia* Miq. Ann. Mus. Bot. Lugd. -Bat. 1 (1863) 9. — *A. beccarii* Ridl. J. Mal. Br. R. As. Soc. 87 (1923) 64. — *A. dasyphylla* var. *urticifolia* (Bl. ex Miq.) Bakh. in Blumea 6 (1947) 367. — *A. dasyphylla* var. *typica* Bakh. -Oostr. in Back. Bekn. Fl. Java, (em. ed.) 7 (1948) fam. 159, 18. — *A. dasyphylla* var. *dasyphylla* Back. & Bakh. Fl. Java, 2 (1965) 710.

Prickly shrub or small tree, often unbranched, to about 5 m high, young parts densely brown pubescent. Leaves forming large rosettes at the summit of the stems, about 1 m long (or more), bi- or tripinnate, the petiole, rhachis and lateral rhachides prickly or unarmed, densely pubescent; leaflets subsessile or petiolule c. 5 mm long (or longer), usually densely pubescent on the lower surface, less dense above, ovate to oblong-ovate, c. 5-14 (18) × 3-5 (10) cm, base rounded to sub-cordate, apex accuminate, margin finely or sometimes coarsely serrulate. Inflorescence a large terminal panicle, densely brown pubescent, ultimate branches arranged racemosely, ending in heads of several sessile flowers.

Distr. Malay Peninsula, Sumatra, West and Central Java. Also northwards to southern China.

Ecol. Primary forest and second growth in deep ravines or open hillsides, occurring from low altitudes (± 100 m) to 2,500 m.

Notes. The capitulate flowers are characteristic (see also under *A. javanica*). The presence of this species in the Malay Peninsula has often been overlooked, though it extends into southern China. Variability is discussed by van Steenis (Bull. Bot. Gard. Btzg. ser 3, 17 (1948) 391).

2\. *Aralia javanica* Miq. Pl. Jungh. 3 (1855) 420.

A shrub or small tree, often unbranched, young parts covered with brown pubescence which persists on the stems and rhachides of the inflorescence as ± patent hairs. Leaves tufted at the ends of the branches, bipinnate; leaflets variable in size, subsessile or the petiolules up to c. 2 cm long, blade ovate to elliptic, up to 18 × 8 cm (usually smaller), both surfaces with sparse short appressed bristly hairs, base cuneate to truncate, apex accuminate, margin finely and unevenly serrulate. Inflorescence a large terminal panicle; the ultimate branches bearing heads (or sub-umbellules) of c. 10 flowers, surrounded by an involucre of small linear bracts.

Distr. Central and West Java (Dieng, Surakarta, G. Papandayan, Mt Malabar, G. Prahu).

Ecol. Mountain forests, 2000-3000 m.

Notes. This imperfectly known species may prove to be a form of the widespread *A. dasyphylla*, from which it appears to differ in the shortly pedicellate flowers, the sparser leaf-tomentum, the more patent hairs on the inflorescence branches and the bracts of the umbellules less thickly enveloped in hairs.

3. *Aralia scandens* (Merr.) Ha in Nov. Sist. Vyssh. Rast. 11 (1974) 229. — *Acanthophora scandens* Merr. in Philip. J. Sc. 13 (1918) 316. — "*Aralia ferox* Miq." King in J. As. Soc. Beng 67 (1898) 45.

Prickly scandent shrub, glabrous, reaching a height of 10 m or more, stems c. 2.5 cm thick. Leaves dispersed (± 30 cm apart), up to 1.5 m long, tri- or quadri-pinnate, prickly on the petiole, rhachides, and sometimes on the leaf veins; leaflets ovate to elliptic-ovate or ovate-lanceolate, base rounded or sub-cordate, apex acuminate, margins finely spinulose-denticulate. Inflorescence a large terminal spiny panicle, the main rhachis to c. 60 cm long, bearing secondary branches singly or in whorls, up to 50 cm long; the ultimate branches 1–4 cm long, subtended by lanceolate bracts, racemosely arranged, ending in umbellules; umbellules 10–20 flowered, pedicels slender 10–12 mm long.

DISTR. Malay Peninsula: Perak, Selangor, Pahang. Sabah: Mt. Kinabalu. Celebes: Menado, South Celebes. Philippines: Luzon, Panay, Catanduanes, Mindanao.

ECOL. Thickets on mountainsides, often near streams, or among second growth. Between 180–1550 m altitude.

Notes. The only species with the habit of a liane, with spaced leaves, and recurved spines. The flowers are whitish or yellowish, and slightly fragrant. Visited by numerous small bees. Fruit fleshy, purple. Scrapings of the bark are applied to wounds and a decoction of the boiled bark is drunk to releave internal pain (Mindanao).

4. *Aralia bipinnata* Blanco, Fl. Filip. (1837) 222. — *A. hypoleuca* Presl. Epim. (1851) 250. — "*A. javanica* Miq" F. Vill. Nov. App. (1880) 101. — *A. glauca* Merr. in Philip. J. Sc. 2 (1907) 291. *A. apoensis* Elmer, Leafl. Philip. Bot. 7 (1914) 2325. *A. bipinnata f. inermis* Steen, in Bull. Bot. Gard. Btzg. ser 3, 17 (1948) 392.

A shrub or small sparsely branched tree to 7 m high, with prickly stems. Leaf to 1.5 m or more long, forming large crowns at the ends of the branches, bipinnate, with some prickles, especially on the petiole or unarmed; leaflets sessile or with a short petiolule, ovate to lanceolate, apex acute or acuminate, base rounded to cordate, margin conspicuously crenate, upper surface green, glabrous, lower surface glaucous, pubescent along the veins and sometimes sparingly on the mesophyll, or almost glabrous throughout. Inflorescence a large terminal panicle, the peduncle and also usually the main branches prickly, the whole either almost glabrous or pubescent; tertiary branches usually 5–10 cm long, ending in umbellules, and bearing a small number of lateral umbellules, or branches; umbellules with many radiating pedicels (about 20–30); pedicels 5–10 mm long.

DISTR. Philippines: Luzon, Leyte, Negros, Mindoro, Mindanao. West New Guinea: Vogelkop. Also in Taiwan and Okinawa.

ECOL. In rather open forests, ravines, and in thickets and second-growth; occurring at about 700 m, but chiefly between 1000–2450 m.

Notes. van Steenis discusses the variability in pubescence and the development of spines (Bull. Bot. Gard. Btzg. ser 3, 17 (1948) 392.

5. *Aralia ferox* Miq. Fl. Ind. Bat. 1, 1 (1856) 750. — *A. filicifolia* Ridl. J. Fed. Mal. St. Mus. 8 (1917) 42.

Spiny shrub or small tree, usually unbranched, to about 10 m high. Leaves forming a large rosette at the summit of the stem, up to about 1 m long, bi- or tri-pinnate, prickly on the petiole, main rhachis, and often on the lateral rhachides; leaflets sessile or petiolules to c. 5 mm, ovate or ovate-oblong, variable in size, base truncate to rounded or cuneate, apex acute acuminate, margin sharply serrate, both surfaces with small bristle-like spines, especially on the veins. Inflorescence a large terminal panicle, 25–50 cm long, glabrous, tertiary branches disposed singly or in sub-verticils, ending in umbellules; flowers about 10–12 per umbellule.

DISTR. Sumatra: West Coast, Mt Kerintje. Java: Gedeh, Patuha and Tangkuban Prahu.

ECOL. In montane scrub and among scattered trees; occurring between 1900-2900 m.

forma *nana* Steen. in Bull. Bot. Gard. Btzg. ser 3, 17 (1948) 394, fig. 1.

Smaller, probably 0.5-1.0 m tall, leaves tri-pinnate, 30 cm long, spiny all over, leaflets 4–13 × 2–7 mm, rhachides of the ultimate pinnae winged.

DISTR. Sumatra: known only from Mt Talang.

ECOL. Growing about 2500 m altitude.

Notes. van Steenis considers this interesting dwarf form to represent the extreme of a series in size variability.

6. *Aralia montana* Bl. Bijdr. (1826) 870. — *Panax armatus* Wall. Cat (1832), 4933 nomen nudum; G. Don Gen. Syst. 3 (1834) 386. — *Aralia montana* var. *acutata* Miq. Ann. Mus. Bot. Lugd. -Bat., 1 (1863) 9. — *A. armata* (Wall.) Seem. Journ. Bot. 6 (1868) 134. — *A. thomsonii* Seem. Journ. Bot. 6 (1868) 134. — *A. montana* var. *crassifolia* Bakh. — Oostr. in Back. Fl. Java (em. ed.) 7 (1948) fam. 159, 18.

A shrub or small tree, frequently unbranched, with prickly stems. Leaves to 1 m or more long, forming large crowns at the ends of the branches, bipinnate, usually with some prickles, especially on the petiole, or unarmed. Leaflets sessile or with a short petiolule, ovate, up to 14 × 7 cm, apex acute to acuminate, base truncate or rounded, oblique in lateral leaflets, margin sharply serrate, upper surface with the remains of a strigose tomentum, often ± rugose, lower surface often with a ± velvety tomentum, or with more harsh hairs ± confined to the veins. Inflorescence a large terminal panicle, the peduncle and branches tomentose, prickles, if any, confined to the peduncle and main rhachis; secondary branches at intervals along the main rhachis, c. 35 cm long, bearing numerous tertiary branches along their length; tertiary branches usually c. 6 cm long, ending in umbellules, and often bearing a number of lateral umbellules; umbellules with many radiating pedicels; pedicels usually 12–15 mm long, occasionally shorter, pubescent. Lobes 5, 5-celled, glabrous.

DISTR. Malay Peninsula, Sumatra, Java, Sarawak, Sabah, Celebes.

ECOL. Primary and secondary forest, bamboo forest and low-lying moist ground, from near sea level to 2600 m.

Notes. This species is considered to include all west Malesian examples with pedicellate flowers and pubescent leaves. This broad concept is contrary to former treatments which have recognized several species (*A. thomsonii, A. armata*). The alliance with *A. chinense* Linn. is also very close. The application of names to this and other Javanese species has been very confused. The position is ably discussed by Koorders and Valeton Bijdr. 7 (1900) 52 et seq. and by van Steenis Bull. Bot. Gard. Btzg Ser 3, 17 (1948) 391. In most specimens the lower leaf surface and the pedicels are densely tomentose, but examples occur in which the leaf is only sparsely hairy and the pedicels may be glabrous. *A. armata* appears to be within the range of viaration of the complex as also does *A. decaisneana* Hance of China. The most aberrant specimens are those with glabrous umbellules which are mostly from Sumatra but also from Java: they may indicate that *A. foliolosa* Seem. should also be included in this complex.

Scanning Electron Microscopical Studies on the Spores of Pteridophytes

XI. The Family Oleandraceae (*Oleandra, Nephrolepis* and *Arthropteris*)

by

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Abstract

The monolete bilateral spores of three genera of ferns belonging to the Oleandraceae (*Oleandra, Nephrolepis* and *Arthropteris*) were examined by scanning electron microscope. It is found that the spores of *Oleandra* are characterized by a large folded perine, and densely echinate exine bearing pointed spines or blunt supporting rods. *Arthropteris* possesses spores with more or less similar perine characteristics, and considering its morphological similarities with those of *Oleandra,* this genus may well be included in the family Oleandraceae. Spores of *Nephrolepis,* on the other hand, being characterized by insulate or verrucose perines, thus resemble more closely those of the Davalliaceae, the closest relative of *Nephrolepis.* However, many of its morphological and anatomical characteristics are so distinctive and unique that it clearly constitutes a natural group by itself, and should, as proposed by Ponce de Leon (1953), be treated as the only member of an independent family, the Nephrolepidaceae.

Introduction

The taxonomic and phylogenetic position of the fern genera *Oleandra, Nephrolepis, Arthropteris* and *Psammiosorus* have long been debated and remain controversial. *Oleandra* Cav. is a genus of the tropics and has about 40 species. It differs from other fern genera in many features, and for that reason its taxonomic position is not fully established. Attributing great importance to the articulation of the stipe to the stem J. Smith (1866) first segregated *Oleandra* from the Aspidiaceae and considered it the sole genus of the new tribe of Oleandreae. After the detailed anatomical study of the Japanese species *O. wallichii* by Ogura (1938), *Oleandra* was considered as an isolated genus, and treated as the only genus in the family Oleandraceae (Ching, 1940). Later, many authors accepted it as a monogeneric family (Dickason, 1946; Ponce de Leon, 1953; Pichi-Sermolli, 1965). Others however, have either treated it as 'a genus incertae sedis' (Bower, 1928), or placed it among many other groups of ferns. Of the latter Diels (1889) arranged it in the independent monotypic Tribus Oleandreae of Polypodiaceae, and Christensen (1938) put it in the monotypic subfamily Oleandroideae of the same family. Still other pteridologists included it in the Dennstaedtiaceae (Holttum, 1947), in the Davalliaceae (Copeland, 1947; Alston, 1956; Tardiue-Blot, 1958), or in the subfamily Oleandroideae of Davalliaceae (Tindale, 1961; Crabbe, Jermy & Mickel, 1975).

The genus *Nephrolepis* Schott has about 30 species distributed in the tropics, Japan and New Zealand. Presl (1836) included *Nephrolepis* in the section Nephrodiariae of his tribe Aspidiaeae. Most workers placed it either in the family Davalliaceae (Ching, 1940; Dickason, 1946; Copeland, 1947), or included it in a separate group placed near the Davalliaceae (Nayar, 1970; Holttum, 1971, 1973). However, Ponce de Leon (1953) established the family Nephrolepidaceae for this group of ferns. *Nephrolepis* is usually classified with *Oleandra* because "they are probably more nearly related together than either is to any other genus" (Holttum, 1954).

Arthropteris J. Smith is a small genus of about 20 species and distributed in the Old World tropics and southwards to Australia and New Zealand. "The species of *Arthropteris* are in utter confusion" (Copeland, 1958). The affinity of *Arthropteris* is not clear either (Holttum, 1966). It has certain characteristics which are similar in some extent, to the genera *Oleandra, Nephrolepis, Davallodes, Elaphoglossum, Thelypteris, Teratophyllum, Ctenitis* and *Tectaria.* It is usually placed near *Nephrolepis,* but may not be its nearest relative (Holttum, 1966).

The monotypic genus *Psammiosorus* C. Chr. of Madagascar is peculiar and shows features in common with *Arthropteris* (Copeland, 1947) and the Davallioid ferns (Christensen, 1932; Holttum, 1966). It is always grouped with the Davallioids or Oleandroids (Pichi-Sermolli, 1965), but its actual taxonomic position and affinities are not clear.

These four genera have in the past and recently been variously grouped (Holttum, 1966, 1971; Nayar, 1970; Sen & Sen, 1973; Crabbe, Jermy & Mickel, 1975): in one family, the Oleandraceae; in two separate families, the Oleandraceae (*Oleandra*) and Davalliaceae (*Nephrolepis, Arthropteris* and *Psammiosorus*) or in more than two families (Oleandraceae, Nephrolepidaceae and Davalliaceae). In view of the controversy regarding the taxonomic problems and phylogenetic relationships of these genera, it was thought that a detailed study of them is a project worthwhile to undertake.

Spores of ferns are becoming increasingly important in fern taxonomy (Nayar, 1964; Wood, 1973; Moe 1974; Liew, 1976c). Because they offer both reliable and stable morphological characters in (i) distinguishing species in some genera, (ii) in differentiating genera, subgenera and characterizing families (Brown, 1960; Liew, 1976b) and (iii) in the tracing of possible phylogenetic relationships and trends of evolution between taxa (Brown, 1960; Sorsa, 1964; Nayar & Dewi, 1968; Wagner, 1974) the present author decided to investigate this character and use it as a means to tackle the problems raised above. Scanning electron microscopical observation is preferred and undertaken because it offers the combined superiority of greater depth of field, high resolution, and visually presents three dimensional topographical information which reveals subtle and spectacular structures of spore surfaces previously unobtainable with the optical microscope.

Materials and Methods

Spores of the three genera of ferns belonging to the Oleandraceae (*Oleandra, Nephrolepis* and *Arthropteris*) were taken either from fresh plant material collected in the fields or from herbarium sheets deposited in many institutions (NY, SING, TAI, KLU and HK; see Table I for details). Fresh fronds were carefully dusted for their spores and spores from herbarium specimens were obtained with the use of clean tooth picks.

Before making scanning electron microscopical observation spores of each species are dispersed in a drop or two of Hoyer's solution (Anderson, 1954) and checked preliminary for their proper identity under an ordinary light microscope. Details of the method of preparation and observation on scanning electron microscope were as described before (Liew, 1976a). Many models of scanning scopes were employed in the present investigation, e.g., JOEL JSM 15, JSM U3, Cambridge S4–10, and Hitachi MSM 4. Black and white photomicrographs were recorded on ordinary 120 negative or on Polaroid films with (105 P/N, 55 P/N) or without (42, 107) negatives. Sizes of spores were measured either in polar x equatorial axes (P x E) or in polar x longest equatorial x shortest equatorial axes (P x E1 x E2). Values given are averages of five to ten readings.

TABLE I. Taxa of Oleandroid ferns studied in the present investigation together with some of their spore characteristics.

Taxon	Locality[1], Collector, Number and Herbarium	Size (PXE)[2] in μ	Sculptine Characteristics[3]
Arthropteris J. Smith			
1. articulata (Brack.) C. Chr.	**Fi**: A. C. Smith 6861 (NY)	28-36 x 40-51	a1; b5, 7, 11; d4[4]
2. beckleri (Hook.) Mett.	**A**: E. F. Constable P3920 (SING)	32-40 x 41-55	a1; b3, 11, 15; d4
3. dolichopoda v.A.v.R.	**NG**: H. W. Simmonds, s.n., Jul. 5, 1937 (SING)	28-38 x 40-52	a1; b3, 6, 15; d4
4. monocarpa (Cardemay) C. Chr.	**E**: R. E. G. Pichi-Sermolli 6781 (KLU)	38-46 x 41-50	a1; b4, 9, 15, 16; d4
5. obliterata (R. Br.) J. Sm.	**Bo**: J. & M. S. Clemens 27383 (NY)	36-50 x 43-64	a1; b3, 8, 10. 11, 15; d4
6. pallisotii (Desv.) Alston	**Fa**: M. T. Kao 3731 (TAI)	30-39 x 45-53	a1; b3, 10, 11, 15; d4
7. repens (Brack.) C. Chr.	**Bo**: J. & M. S. Clemens 29568 (SING)	34-44 x 45-58	a1; b10, some 12, 15; d4
8. tenella (Forst.) J. Sm.	**A**: M. S. Clemens, s.n., Jan., 1945 (NY)	45-56 x 50-65	a1; b10, 11, 13; d4
9. wollastonii (Ridl.) Holttum	**Ph**: E. B. Copeland 155 (SING)	31-43 x 41-54	a1; b3, 10, 16; d4
Nephrolepis Schott			
10. acutifolia (Desv.) Christ	**Ma**: B. E. G. Molesworth-Allen 2575 (SING)	20-24 x 27-33	b2, 3, 17
11. biserrata (Sw.) Schott	**Fa**: F. S. Liew 10197 (TAI)	18-24 x 23-29	b2, 3, 17
12. cordifolia (L.) Presl	**Ma**: E. A. Turnau 839 (KLU)	20-25 x 23-30	b2, 3 or 4, 17, some 20
13. davallioides (Sw.) Kze.	**Ma**: B. C. Stone 7244 (KLU)	21-27 x 25-32	b2, 3 or slightly 3, 17
14. dicksonioides Christ	**Ma**: B. C. Stone 5895 (KLU)	20-23 x 29-33	b2, 3, 17
15. exaltata (L.) Schott	**Hi**: C. N. Forbes 2108M (NY)	23-29 x 30-37	b2, 3, 17; d4
16. falcata (Cav.) C. Chr.	**Ma**: R. E. Holttum 9820 (SING)	18-22 x 24-28	b2, 3, 17; d4
17. hirsutula (Forst.) Presl	**Fa**: F. S. Liew 9060 (TAI)	18-25 x 28-35	b2, 18; d4
18. lauterbachii Christ	**NG**: Butten, s.n., 1919 (SING)	17-21 x 26-32	b2, slightly 3, 19
19. pectinata (Willd.) Schott	**CR**: W. C. Burger & R. L. Lieser 6854 (NY)	20-25 x 26-38	b2, 3; d4[5]
20. radicans (Burm.) Kuhn	**Ma**: A. Samat 550 (KLU)	17-22 x 25-31	b2, 18; d4
Oleandra Cavanilles			
21. madagascarica Bonap.	**Mr**: B. C. Stone 7883 (KLU)	25-30 x 30-40	b8, 11; c13; d4
22. neriiformis Cav.	**Ph**: B. F. Henaez, s.n., Nov. 16, 1970 (TAI)	30-36 x 38-45	b5, 11, 12, 21; c12 or 14; d4
23. pistillaris (Sw.) C. Chr.	**Ma**: S. C. Chin 181 (KLU)	31-38 x 45-55	b11, 12; c14; d4
24. undulata (Willd.) Ching	**Hn**: F. A. McClure 20061 (NY)	26-31 x 30-37	b5, 12, 21; c14; d4
25. wallichii (Hk.) Presl	**Fa**: M. T. Kao 6317 (TAI)	25-33 x 37-44	b12 &/or 13; c14; d4[6]

[1] **A**, Australia; **Bo**, Borneo; **CR**, Costa Rica; **E**, Ethiopia; **Fi**, Fiji; **Fa**, Formosa; **Hi**, Hawaii; **Hn**, Hainan; **Ma**, Malaya; **Mr**, Madagascar; **NG**, New Guinea; **Ph**, Philippines.

[2] PXE = Polar axis x Equatorial axis.

[3] *a*. perine; *b*. same, outer layer; *c*. same, inner columnar layer; *d*. exine layer.
1. thick, 2. thin, 3. rough (surface), 4. smooth, 5. lophate (with large polygons); 6. with processes, 7. processes short, rounded, 8. processes small, short, 9. with many folds, 10. with amorphous or irregular structures (raised ridges &/or irregular foldings), 11. with many holes; 12. spines short, pointed, 13. spines long (up to 5 μ), pointed, 14. blunt clubs (up to 3 or 4 μ tall); 15. easily sloughed off, 16. easily cracks open; 17. with insulate, broad, interconnected ridges or verrucae, 18. ridges or verrucae insulate, small, 19. ridges or verrucae insulate, large; 20. verrucae or tubercules very prominent and protruding, 21. same, especially in lacuna, and some forming raised ridges.

[4] Spores appear similar to the spores of *Oleandra* species. [5] Surface almost without ridges. [6] Sculpture of spores rather variable.

Results

The sizes and general characteristics of the spores of all the species of these Oleandroid genera studied in the present investigation are given in Table I.

The insulate or verrucose spores of *Nephrolepis* clearly form a natural group by themselves (Plates I and II). These ellipsoid bilateral spores are monolete and mostly concavo-convex in lateral view. A few of them are plano-convex. The average size of the spore measures about 17–29 x 23–38 x 14–29 μ. Under the SEM, a broken outer sporoderm will reveal the inner exine layer of the spore, which is psilate, slightly scabrate or undulating (Plate I, fig. 8). The laesura is slightly raised, thin and with a short ridge in some species (e.g., in *N. pectinata* and *N. davallioides*) or thick and forming long and rough ridges in others (e.g. in *N. acutifolia* and *N. biserrata*). The sculptine or sporoderm has on its surface elements of various sizes, from small grains or humps to large tubercules, or with irregular excrescences or raised ridges of various sizes.

The ellipsoid spores of *Oleandra* are totally different from *Nephrolepis* (Plates III and IV). They are monolete bilateral spores, and are plano-convex to slightly biconvex in lateral view. The amb is oblong in shape. All the spores have a thick, prominent, loose and wrinkled perine which anastomoses to form regular or irregular polygons or lophate sculptures. Depending upon the species concerned, the perine may have spinulose, blunt or dentate excrescences. The size of the spore is 25–42 x 30–55 x 26–32 μ. Scanning electron micrographs of broken sporoderms reveal that the outer layers are built on stilts, and are supported by numerous rods connected to the layer(s) down below. These micrographs also reveal the smoothness of the inner exine in many cases (Plate IV, fig. 40). Spores of *Oleandra* may differ in sculptural details, even within the same species, but they nevertheless form a group with a unique and distinctive general pattern.

Spores of *Arthropteris* have a thick perine of various sculpturing ornamentations (Plates V and VI). Foldings may be high or low in profile, and are covered with minute projections or interlacing networks. Some *Arthropteris* spores (e.g. *A. articulata*) closely resemble those of *Oleandra* species. The outer perine of most of the spores of *Arthropteris* sloughs off easily, leaving behind the naked exine with smooth surface and laesura. The size of the spores range 28–56 x 40–65 x 25–30 μ. It is ellipsoid and sometimes roundish in polar view, and plano-convex to concavo-convex in lateral view.

Discussion

I. *Nephrolepis*

From our studies on eleven taxa of *Nephrolepis* gathered from various parts of the world it is demonstrated that the bilateral spores of *Nephrolepis* species are rather uniform and form a clear-cut group by themselves. They have thin perine and verrucose sculptine with elevations of various sizes, from slightly raised ridges to conspicuous tubercules.

In the literature, spores of many species of *Nephrolepis* have been studied. Holttum (1954) mentioned that spores of *Nephrolepis* have slightly and irregularly roughened surfaces, and are without distinctive markings. Hannig (1911) pointed out that "a perispore is unlikely to occur" in *Nephrolepis* (*N. exaltata*). This is contradicted here as shown in Plate I, fig. 8, which clearly shows the presence of an outer layer. Among the many authors who have examined the spores of *Nephrolepis exaltata* (L.) Schott was Selling (1946) who investigated Hawaiian species and described it as having very irregular warts and short, irregular ridges, with a size of 24–28 x 41–50 μ. Earlier workers have similarly investigated the spores of this species but did not mentioned the sculpture patterns. Marquesan (southeastern

Polynesia) spores of this taxon are ± 34 μ in length, and with the surface conspicuously tuberculate (Brown & Brown, 1931). Erdtman and Sorsa (1971) described the spores from British West Indies as convex-plane, 22 x 37 x 23 μ (perine not included) with the laesura about 21 μ, and the perine similar to that in *N. biserrata.* The exine stratification is obscure. Spores from North America (Florida) are subpsilate to tuberose, ellipsoid, monolete, and measure 38–55 x 21–31 μ (Kremp & Kawasaki, 1972).

Harris (1955) described the spores of the New Zealand *Nephrolepis cordifolia* as having verrucate surfaces with elongated projections and of 18–40 μ. Spores of the same species in India (Darjeeling) are reported to be bilateral and possess a very thin perine forming small humps (Sen & Sen, 1973).

Some other species of *Nephrolepis* have also been described by Erdtman and Sorsa (1971). For example, the spores from Java of *N. davallioides* (labelled as *N. acuminata*) are provided with a more or less verrucose, dark brownish, *cf.* perinous layer *ca* 1.0 μ broad. The spores are reported to be concavo-convex and of 17 x 34 x 23 μ in size (perine not included). The Ceylonese species of *N. biserrata* has convex-concave spores and measured 23 x 39 x 26 μ (perine included). It has a perine *ca* 1.5 μ thick, is verrucose; warts are dark brownish *ca* 1.3 x (2.0–6.0) μ high. The Japanese species of *N. falcata* has a more or less perinous thickening which is columnar, wart-like and about (3.0–4.0) x (4.0–7.0) μ. The spores are 30 x 45 x 35 μ (perine not included). The Ceylonese species of *N. hirsutula* has convex-plane or slightly biconvex spores, 21 x 35 x 25 μ thick and finely verrucose.

The bilateral and more or less verrucate sculptine patterns of the spores is similar, if not identical, in all species of *Nephrolepis* so far examined, and thus form a rather homogeneous group by themselves. Though a few of the *Nephrolepis* species are remarkably variable, poorly defined or with bizarre features, the uniformity and uniqueness in their vegetative characters, however, has clearly demonstrated the naturalness of the whole group (Pichi-Sermolli, 1965). "It therefore constitutes a clearly natural genus" (Copeland, 1958).

Traditionally *Nephrolepis* has been associated with the Davallioids, Dicksonioids or the Aspidioid ferns. Copeland (1947) commented that this genus has many morphological and anatomical characters in common with the Davalliaceae and affinity seems certain, but many are not close. In chromosome number (n = 41), scales (peltate) and indusium (reniform), *Nephrolepis* resembles *Oleandra;* but in many other characters, such as habit, anatomy of the stem and stipe, articulation of the stipe, the feature of the rhizome, venation, position of the sori and structure of the spores, they differ considerably (Pichi-Sermolli, 1965). However, as a group, this genus has spores similar to its closest relative of Davalliaceae ferns, *Davallia, Humata, Araiostegia, Leucosteiga* and *Davallodes,* all of which possess spores with markings of varying degree. Undoubtedly, the phylogenetic position of *Nephrolepis* is thus in the Davalliales.

Since features of some *Nephrolepis* species are similar to some of the fern genera and families, especially members of the Davalliaceae, and have in the meantime shown to be distinctive in other important characters, it might be better to group all the species of *Nephrolepis* in a separate and distinctive group, the family Nephrolepidaceae, as was suggested by Ponce de Leon (1935). The phylogenetic affinity of this family is with the family Davalliaceae.

II. *Oleandra*

The bilateral spores of the genus *Oleandra* are also homogenous in having a distinctive, thick, smooth or wrinkled perine with a few or many protruding folds. The folds may form an irregular network having large meshes (lophate). Spinulose excrescences distributed on the surface may be few or numerous. Usually these are broader and thicken at the base tapering to sharp apices. Some of these structures have blunt rods.

In the literature, all workers who have done palynological work on *Oleandra* have reported similar findings. For example, Erdtman and Sorsa (1971) described the convex-plane spores of *O. musifolia* of Ceylon as being 28 x 40 x 30 μ (perine not included), the perine with folds of *ca* 5.0–10.0 μ high, and anastomosing to form irregular polygons with broadly conical and blunt crests. The perine is sparsely spinulose or dentate. It is provided with densely spaced, intra-perinous rods about (2.0–5.0) x (0.5–1.0) μ and spaced *ca* 1.0–2.0 μ apart. As described by Kremp and Kawasaki (1971) the ellipsoid spores of the Javanese *Oleandra neriiformis* measure 43–63 x 36–49 μ, and are monolete and perisporate or psilate (in this case, presumably the perine has sloughed off!). Erdtman (1957) also illustrated the spore of this species. Copeland (1947) mentioned that the spores are bilateral or angular by shrinkage of the epispore and are apparently smooth. Sen and Sen (1973) illustrated and described the spores of Indian species of *O. wallichii* as monolete, bilateral plano-convex in lateral view, and oblong in polar view. The perine is said to be folded and spiny.

The habit of growth of *Oleandra* is almost unique and has been described as the only shrubby fern, although all species included in it are not necessary shrubby (Nayar, Bajpai & Chandra, 1968). The genus also shows homogeneity in many features, such as spore sculpture, etc. It differs from all other ferns in the anatomy of the stem, the position of the sori, the presence of peculiar aerial roots, and also in the structure of the spores (Pichi-Sermolli, 1965; Braggio, 1966). There are thus enough justification to treat *Oleandra* as an isolated genus in the independent family Oleandraceae Ching ex Pic. Ser., as agreed by many pteridologists (J. Smith, 1866; Diels, 1889; Christensen, 1938; Ching, 1940).

The ancestry of *Oleandra* is unknown (Copeland, 1947). Its remarkable resemblance in many features with some species of *Davallia* and *Humata* suggests clearly its close affinity with the Davallioid ferns. Nowadays, most workers place it under the Davalliales.

In ferns, bilateral perinate spores are characteristic of the Aspidioids, Asplenioids, Lomariopsidoids and the Thelypterioid ferns, and the presence of spinulose excrescences over the perine is found especially common among the Aspidioid genera (Nayar & Devi, 1964; Nayar & Kaur, 1965). When the characters of the spores are taken into consideration with anatomical, morphological and cytological features, it is suggested that this unique group of ferns has a closer phylogenetic relationship with the Aspidioid ferns, as has been suggested by many investigators such as Presl (1836), Dickason (1946), Nayar, Bajpal and Chandra (1968), and Pichi-Sermolli (1965). The last author has also emphasized that its affinity in the second place is with the Polypodiales, rather than with the Dicksoniales to which affinity was alluded by most authors in the past.

III. *Arthropteris*

Copeland (1947) referred to the spores of *Arthropteris* as oblong and with epispore. In his study on the genus of *Arthropteris* in Malesia, Holttum (1966) mentioned that the spores of this genus have folded perispores.

However, there are some differences of opinion concerning the sculptine structures even within the same species. For example, Harris (1955) reported the New Zealand species of *A. tenella* as having bilateral, winged spores with cristate perispore separated from the spore wall and both of these structures differ in contour. The surface is striate-scabrate and with a few crests. The crests, when seen in oblique or transverse view, form irregular, almost spinulose projections, 9–14 μ in height. The contour or outline is deeply resected. However, spores of the same species from the same country were reported by Sen and Sen (1973) to be monolete-bilateral and possessing a thin and granulose (in the description) or verrucose (in the diagram) perine. Furthermore, Kremp and Kawasaki (1972) reported this same species to have monolete ellipsoid spores of 34–62 x 27–43 μ, and having a thin perine with psilate surface. Our SEM investigation on *A. tenella*, however, confirmed the correct observation and description of Harris (1955). The verrucose spores of Sen and Sen (1973) were most probably due to contamination or observation on abnormal spores. Those observations by Kremp and Kawasaki (1972) could have been either too immature or mature spores with ablated perine, a phenomenon frequent among many *Arthropteris* species.

Spores of several other species of *Arthropteris* have been studied e.g. *A. altescandens* of Juan Fernandez was reported to have spores with short elliptic to subcircular amb and as having a very thin (*ca* 0.3 μ) and folded perine (folds up to 10 μ high). Those of *A. obliterata* (labelled as *Nephrolepis ramosa* Moore) of Ceylon was said to have no perine, were biconvex and 39 x 55 x 40 μ. The psilate spores of *A. monocarpa* of Africa and Madagascar and the spores with a large and folded perine and smooth exine of the African (Congo) *A. orientalis* have also been studied by Braggio (1966).

The affinity of *Arthropteris* is not clear. Copeland (1947) placed it tentatively in the Oleandra-Davallia series. Collective similarities in aspects of frond structure, articulation of pinnae, terminal sori on veins, are evidence of affinity with the *Nephrolepis*. Holttum (1966) does not think that *Nephrolepis* is its nearest relative despite the placement near *Arthropteris*. He, however, agreed with J. Smith in accepting *Arthropteris* as a natural genus, and believed that its peculiar combination of characters may give significant hints as to interrelationships among various groups of ferns. But, he is not yet clear as to how such a relationship may best be formally expressed in a scheme of classification. From studies on the spores of two *Arthropteris* species of Africa and Madagascar, Braggio (1966) emphasized that *Arthropteris* differs from both Oleandraceae and Davalliaceae, and that it ought to be referred to the order of Aspidiales because of its spore characteristics (with psilate exine and a wide and thin perine, with or without ornamention).

From our observation on spore structure *Arthropteris* species is closer to the Oleandroids rather than to the *Nephrolepis* and Davalliaceae. This is especially evident from the spores of *A. articulata* which are almost indistinguishable from those of some *Oleandra* species (Plate V, figs. 46–49). Spores of other species of *Arthropteris* may not be more distant as they possess a smooth exine and a thick and variously folded perine with different sculptured patterns (Plate VI). However, they still display numerous structural features in common with the *Oleandra* spores. Pichi-Sermolli (1965) also pointed out the similarities of both genera, such as the articulation of the stipe, the shape of the sorus and indusium, the presence of a wide perine, and the chromosome number. When everything is taken into consideration, the disposition of *Arthropteris* in the Davalliales is undoubtedly natural.

The proper systematic position of the peculiar monotypic genus *Psammiosorus* (endemic in Madagascar) is not fully established (Christensen, 1932; Copeland, 1947; Tardieu-Blot, 1964; Pichi-Sermolli, 1965; Braggio, 1966; Holttum 1966).

In conclusion, the family Davalliaceae sensu Copeland (1947) can now be envisaged as the order Davalliales which comprises three natural groups, the family Davalliaceae *s.s*, containing more strictly Davallioid genera, the family Oleandraceae, with the genera *Oleandra* and *Arthropteris*, and the family Nephrolepidaceae, with the monotypic genus *Nephrolepis*. The proper phylogenetic position of *Psammiosorus* cannot be proposed until further study. At the level of the Order, the affinity of the Davalliales is close to the Aspidiales.

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Literature Cited

Alston, A. H. G. 1956. The subdivision of the Polypodiaceae. *Taxon,* **5**: 23–25

Anderson, L. E. 1954. Hoyer's solution as a permanent mounting medium. *Bryologist,* **57**: 242–244.

Bower, F. O. 1928. *The Ferns (Filicales).* Vol. III. The Leptosporangiate Ferns. Cambridge Univ. Press, Cambridge.

Braggio, G. 1966. Morfoligia delle spore sistematica delle Davalliales. *Webbia,* **21**: 725–767.

Brown, C. A. 1960. What is the role of spores in fern taxonomy? *Amer. Fern. J.,* **50**: 6–14.

Brown, E. D. W. & F. B. H. Brown. 1931. Flora of Southeastern Polynesia. II. Pteridophytes. *Bishop Mus. Bull.* 89.

Case, I. M. 1932. The development of the sorus in some species of *Nephrolepis* with some observations on points of anatomical interest. *Trans. Roy. Soc. Edinb.,* **57**: 258–276.

Ching, R. C. 1940. On the natural classification of the family Polypodiaceae. Sunyatsenia, **5**: 201–268.

Christensen, C. 1932. The Pteridophyta of Madagascar. p. 70–74. Hayerup's Boghandel, Kobenhavn.

—————— 1938. Filicinae. In F. Verdoorn (ed.), Manual of Pteridology. p. 522–550. Nijhoff, the Hague.

Copeland, E. B. 1947. *Genera Filicum.* Chronical Botanica, Waltham, Mass.

—————— 1958. *Fern Flora of the Philippines.* Vol. I. Nat. Inst. Sci. Tech., Manila.

Crabbe, J. A., A. C. Jermy & J. T. Mickel. 1975. A new generic sequence for the pteridophyte herbarium. *Fern Gaz.,* **11**: 141–162.

Dickason, F. G. 1946. A phylogenetic study of the ferns of Burma. *Ohio J. Sci.,* **46**: 73–108.

Diels, L. 1899. *Polypodiaceae.* In A. Engler & K. Prantl, Die Naturlichen Pflanzenfamilien, I (4): 139–339. Engelmann, Leipzig.

Erdtman, G. 1957. *Pollen and Spore Morphology/Plant Taxonomy.* (Corrected reprint 1972) Hafner Pub. Co., New York.

Erdtman, G. & P. Sorsa. 1971. Pollen and Spore Morphology/Plant. Taxonomy. IV. Pteridophyta. Almqvist & Wiksell, Stockholm.

Hannig, E. 1911. Uber das Vorkommen von Perisporien bei den Filicinen nebst Bemerkungen uber die systematische Bedeutung derselben. Flora, **103**: 321–346.

Harris, W. F. 1955. A manual of the spores of New Zealand Pteridophyta. New Zealand Dept. Sci. Ind. Res. Bull. **116**: 1–186.

Holttum, R. E. 1947. A revised classification of leptosporangiate ferns. Bot. J. Linn. Soc., **53**: 123–158.

——————— 1949. Classification of ferns. Biol. Rev., **24** 267–296.

——————— 1954. A Revised Flora of Malaya. Vol. II. Ferns. (2nd ed., 1968) Government Printing Office, Singapore.

——————— 1966. The genus *Arthropteris* J. Sm. in Malesia. Blumea, **14**: 225–229.

——————— 1971. The family names of ferns. Taxon, **20**: 527–531.

——————— 1973. Introduction to Pteridophyta (and) Family names of Pteridophyta (+ all pteridophyte entries). In J. C. Willis, A Dictionary of the Flowering Plants and Ferns, 8th ed. Revised by H. K. Airy Shaw. Cambridge Univ. Press, Cambridge.

Kremp, G. O. W. & T. Kawasaki. 1972. The Spores of the Pteridophytes. Hirokawa Book Co., Tokyo.

Liew, F. S. 1976a. Scanning electron microscopical studies on the spores of Pteridophytes. I. The genus *Pyrrosia* Mirbel (Polypodiaceae) found in Taiwan. Quart. J. Taiwan Mus., **24**: 191–216.

——————— 1976b. A scanning electron microscopical study on the spores of *Lycopodium* found in Taiwan. Sci. Agr., **24**: 162–172.

——————— 1976c. Scanning electron microscopical studies on the spores of pteridophytes. VII. The family Plagiogyriaceae. Taiwania, **21**: 37–49.

Moe, D. 1974. Identification key for trilete microspores of Fennoscandian Pteridophyta. Grana Palyn., **14**: 132–142.

Nayar, B. K. 1964. Palynology of modern Pteridophyta. In B. K. Nair (ed.), Advances in Palynology, p. 100–141. United Block Printers, Lucknow.

——————— 1970. Classification of homosporous ferns. *Taxon,* **19**: 229–236.

Nayar, B. K. & S. Devi. 1964. Spore morphology of Indian ferns. I. Aspidiaceae. *Grana Palyn.,* **5**: 80–120.

——————— 1968. Spore morphology of the Pteridaceae. IV. Taxonomic and phyletic considerations. *Grana Palyn.,* **8**: 517–535.

Nayar, B. K. & S. Kaur. 1965. Spores morphology of the Lomariopsidaceae. *J. Palyn.,* **1**: 10–26.

Nayar, B. K., N. Bajpai & S. Chandra. 1968. Contributions to the morphology of the fern genus *Oleandra. Bot. J. Linn. Soc.,* **60**: 265–282.

Ogura, Y. 1938. Anatomy and morphology of *Oleandra wallichii* (Hk.) Presl. *Jap. J. Bot.,* **9**: 193–211.

Perez Arbelaez, E. 1928. Die naturliche Gruppe der Davalliaceen (Sm.) *Kaulf. Bot. Abhandl. K. Geobel,* **14**:1–96.

Pichi-Sermolli, R. E. G. 1959. *Pteridophyta.* In W. B. Turril (ed.), Vistas in Botany, p. 421–493. Pergamon Press, London.

——————— 1965. Adumbratio Florae Aethiopicae. II. Oleandraceae. *Webbia,* **20**: 745–769.

———— 1970. A provisional catalogue of the family names of living pteridophytes. *Webbia,* **25:** 219–297.

Pokrowskaila, I. M. 1958. Analyse Pollingue. *Ann. Serv. Inform. Geol. B.R.G.G.M.,* **24**: 1–435.

Ponce de Leon, A. 1953. Nociones de botanica Sistematica. VIII. Division Pteridophyta. *Revta Soc. Cuban Bot.,* **10**: 37–45.

Presl, C. B. 1836. *Tentamen Pteridographiae.* Haase, Prague.

Selling, O. H. 1946. Studies in Hawaiian pollen statistics. Part I. The spores of the Hawaiian pteridophytes. *Bishop Mus. Spec. Pub.* **37**: 1–87.

Sen, T., U. Sen & R. E. Holttum. 1972. Morphology and anatomy of the genus *Davallia, Araiostegia* and *Davallodes,* with a discussion on their affinities. Kew Bull., **27**: 217–243.

Sen. U. & T. Sen. 1973. Anatomical relationships between the *Oleandra* and *Nephrolepis* groups. Bot. J. Linn. Soc. 67, Suppl. **1**: 155–172.

Smith, J. 1866. *Ferns, British and Foreign.* p. 73. London.

Sorsa, P. 1964. Studies of the spore morphology of Fennoscandian fern species. *Ann. Bot. Fenn.,* **1**: 179–201.

Tardieu-Blot, M. L. 1958. *Polypodiacees (sensu lato). Dennstaedtiacees. Aspidiacees.* In H. Humbert (ed), Flore de Madagascar et des Comores (Plantes Vasculaires). Fam. 5. **1**: 1–391. Typographie Firmin-Didot, Paris.

———— 1964. Sur les spores de Davalliaceae et Vittariaceae Malgaches. *Pollen Spores,* **6**: 537–544.

Tindale, M. D. 1961. Pteridophyta of South Eastern Australia. Davalliaceae. *Contr. N.S. Wales Nat. Herb. Fl.* Ser. **208–211**: 1–4.

Wagner, W. H., Jr. 1974. Structure of spores in relation to fern phylogeny. *Ann. Missouri Bot. Gard.,* **61**: 332–353.

Walker, J. W. & J. A. Doyle. 1975. The bases of Angiosperm phylogeny: Palynology. *Ann. Missouri Bot. Gard.,* **62**: 664–723.

Wood, C. C. 1973. Spore variation in the Thelypteridaceae. *Bot. J. Linn. Soc.* **67**. Suppl. **1**: 191–202.

Scale for figures of Plates I to VI

For values of magnifications in the legend, *1 cm* on the micrographs approximates to:—

67μ	(x 150)	15μ	(x 750)	6.7μ	(x 1500)
40μ	(x 250)	10μ	(x 1000)	4μ	(x 2500)
20μ	(x 500)	8μ	(x 1250)	2.5μ	(x 4000)

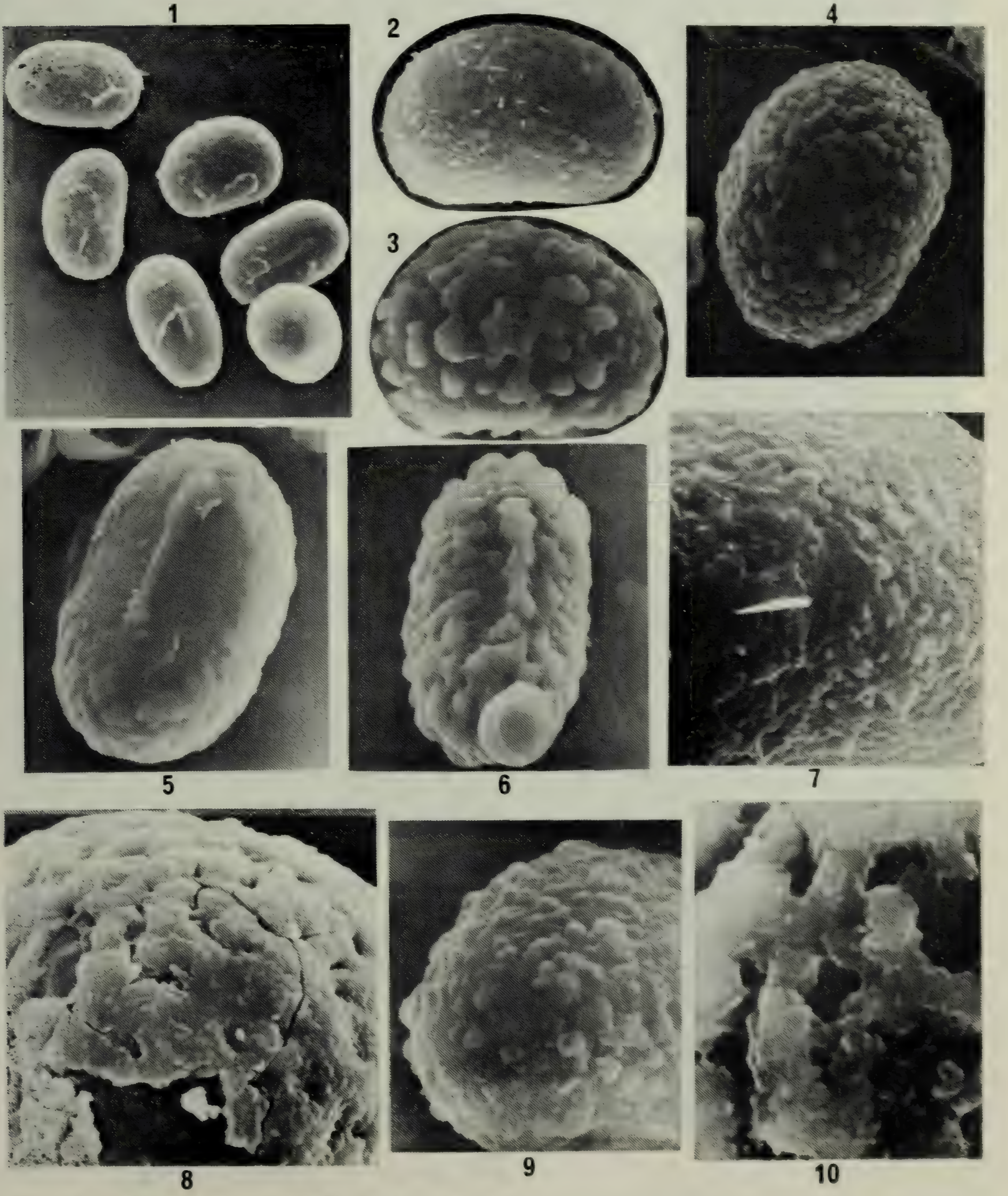

Plate I. Spore characteristics of *Nephrolepis.*

Figs. *1*: Group of spores shown at different views; *2, 3, 4*: typical bilateral spores of *Nephrolepis,* with surfaces more or less smooth (*2*) and rough (*3, 4*); *5, 6*: spores in polar view, showing laesurae thin (*5*) and thick (*6*); *7-10*: close-up views of the spore surfaces, showing more or less smooth (*7*), moderately roughened (*8, 9*) and rough (*10*) surfaces. Note that *8* is of a broken spore of *N. exaltata,* showing the outer rough surface (perine) and the inner smooth surface (exine).

N. pectinata: figs. *1* (x 750), *2* (x 1000), *7* (x 2500); *N. cordifolia*: *3* (x 1500), *5* (x 1500); *N. hirsutula*: *4* (x 1250), *9* (x 2500), *10* (x 5000); *N. biserrata*: *6* (x 1500); *N. exaltata*: *8* (x 2500).

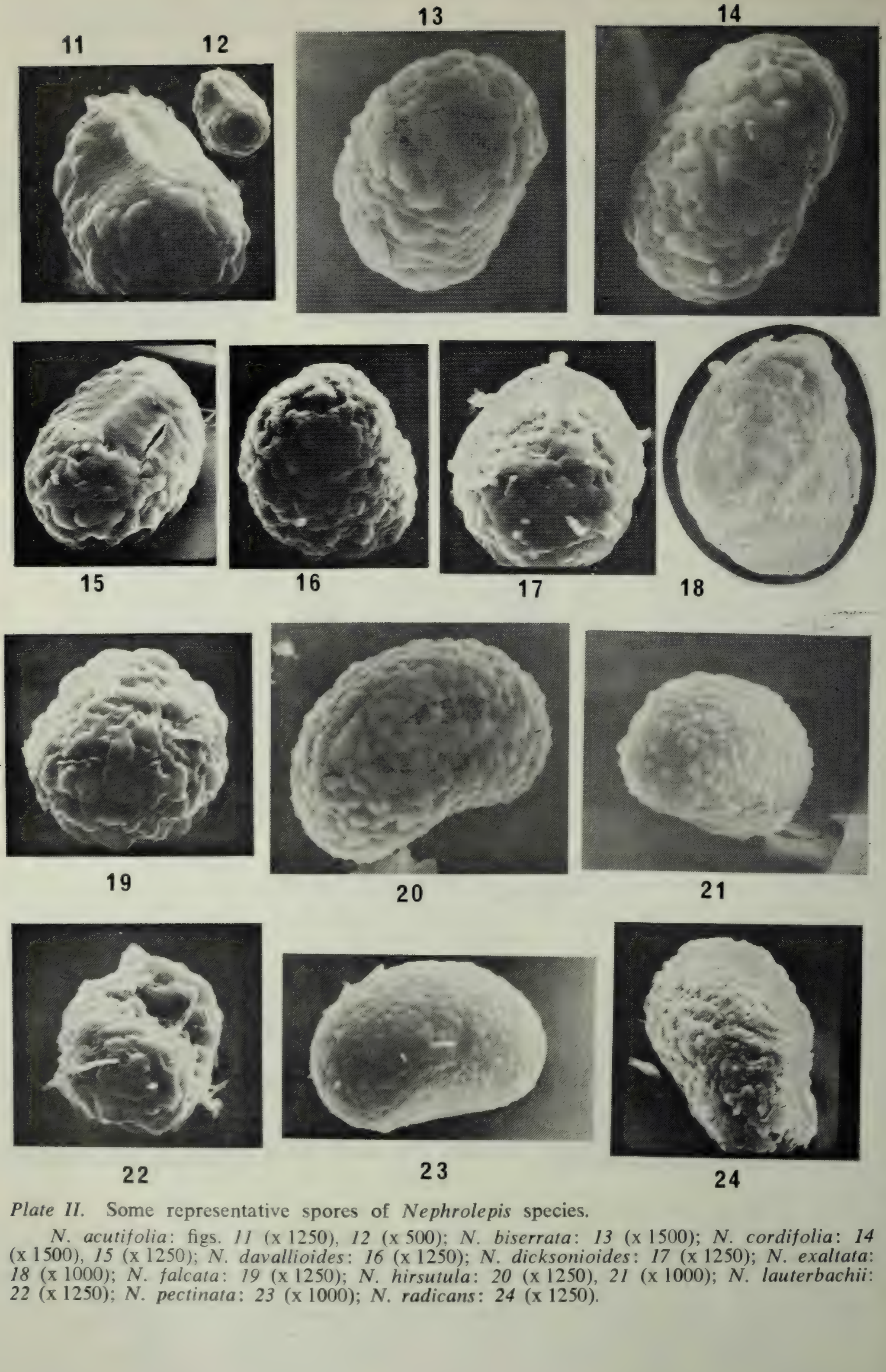

Plate II. Some representative spores of *Nephrolepis* species.

N. acutifolia: figs. *11* (x 1250), *12* (x 500); *N. biserrata*: *13* (x 1500); *N. cordifolia*: *14* (x 1500), *15* (x 1250); *N. davallioides*: *16* (x 1250); *N. dicksonioides*: *17* (x 1250); *N. exaltata*: *18* (x 1000); *N. falcata*: *19* (x 1250); *N. hirsutula*: *20* (x 1250), *21* (x 1000); *N. lauterbachii*: *22* (x 1250); *N. pectinata*: *23* (x 1000); *N. radicans*: *24* (x 1250).

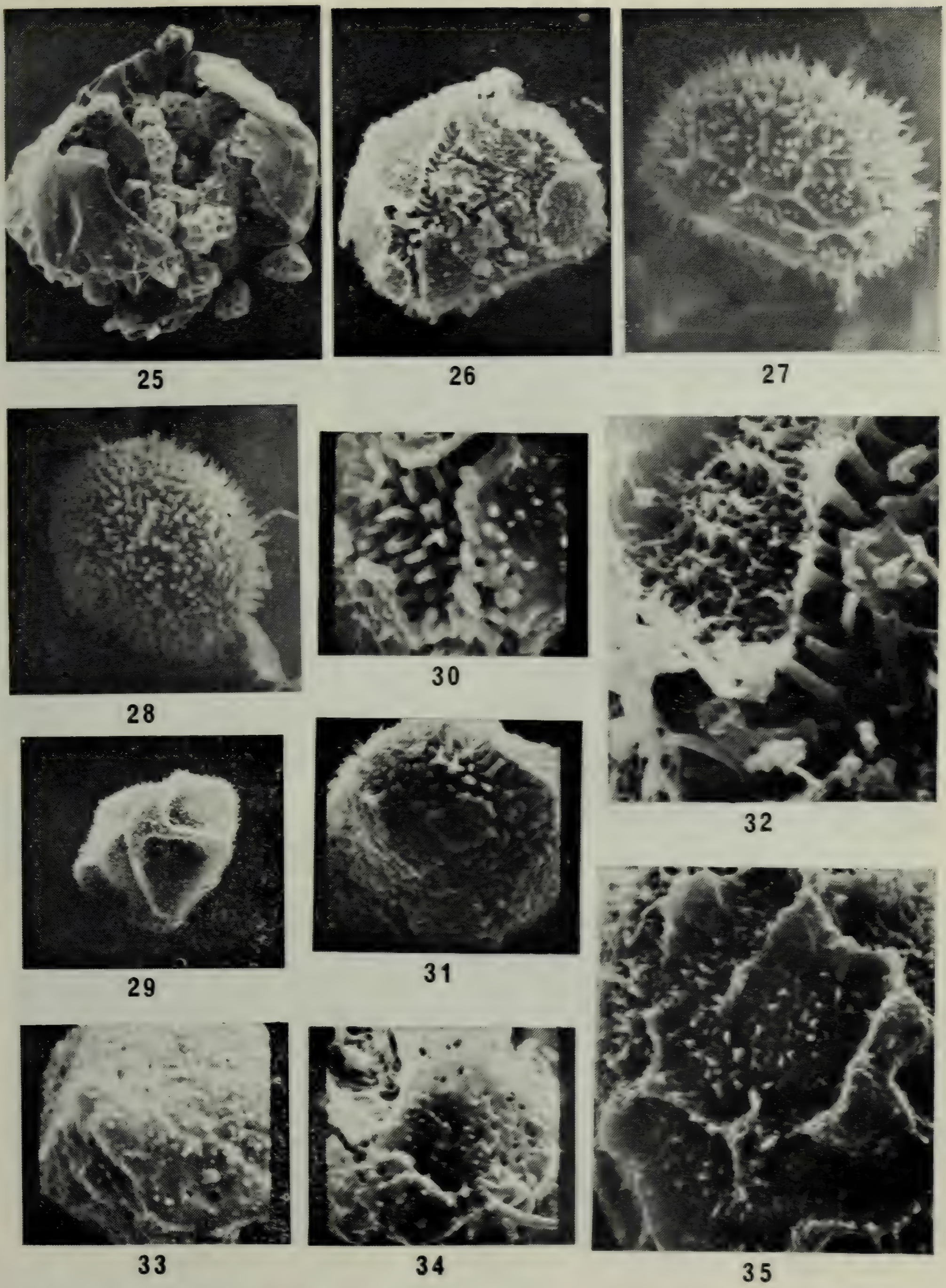

Plate III. Spore characteristics of *Oleandra.*

Figs. *25*: Group of spores within a broken sporangium; *26*: typical structure of a spore with broken perine; *27*: a partly spinulose and partly ridged spore; *28*: a wholly spinulose spore; *29*: another type of spinulose spore with thick ridges; *30, 31, 32*: close-up views of some broken perines, showing erect blunt rods and details of surrounding structures; *33, 34*: close-up views of some unbroken perines, showing holes and short spines; *35*: structure of the short spines, etc. on the perine.

O. undulata: 25 (x 150), *26* (x 1000), *29* (x 500), *31* (x 1250), *32* (x 4000), *35* (x 2500); *O. wallichii*: 27 (x 1000), *28* (x 750); *O. madagascarica*: *33* (x 500); *O. pistillaris*: *30* (x 2500), *34* (x 500).

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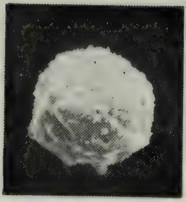

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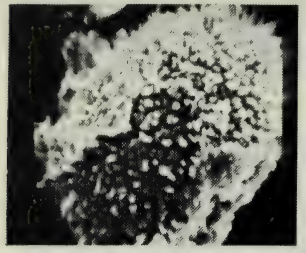

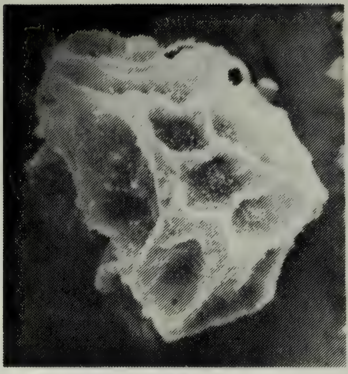

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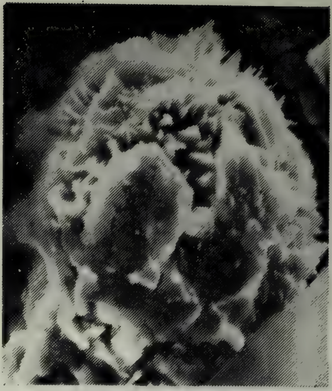

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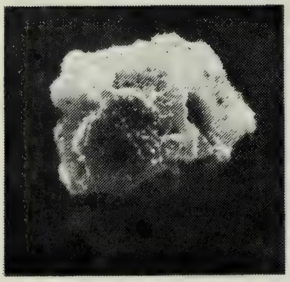

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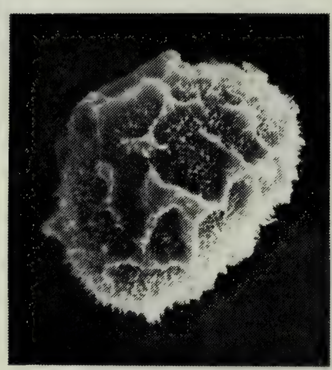

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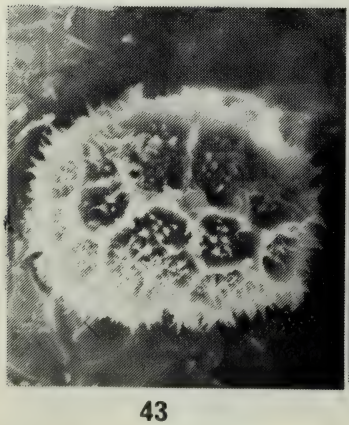

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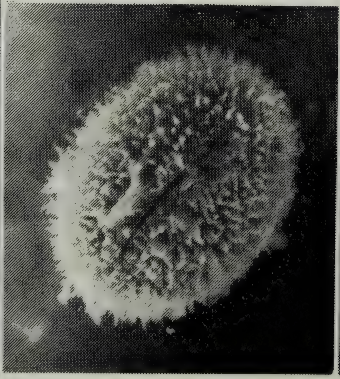

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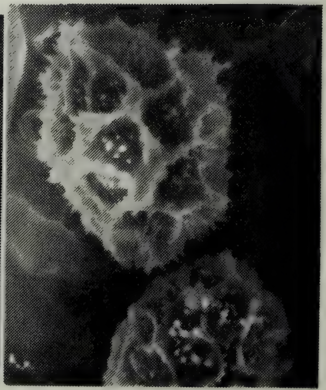

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Plate IV. Some representative spores of *Oleandra* species.

O. Madagascarica: figs. *36* (x 500), *37* (x 1250); *O. neriiformis*: *38* (x 1000), *39* (x 1500), *40* (x 1000); *O. pistillaris*: *41* (x 500); *O. undulata*: *42* (x 1000); *O. wallichii*: *43* (x 1000), *44* (x 1000), *45* (x 750).

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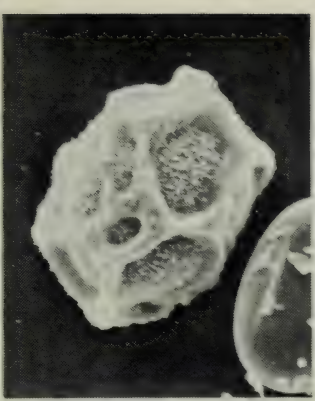

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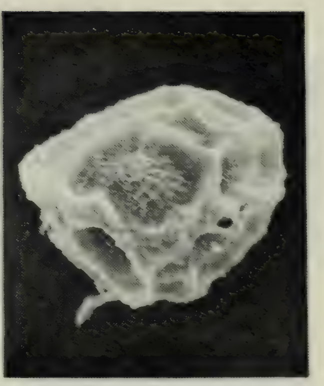

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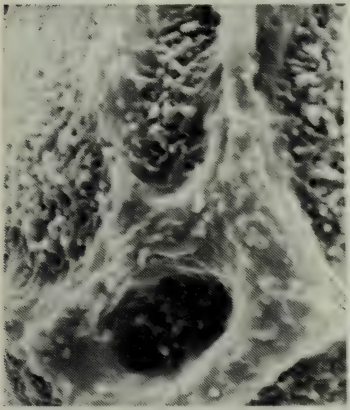

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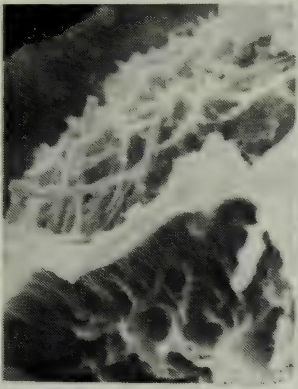

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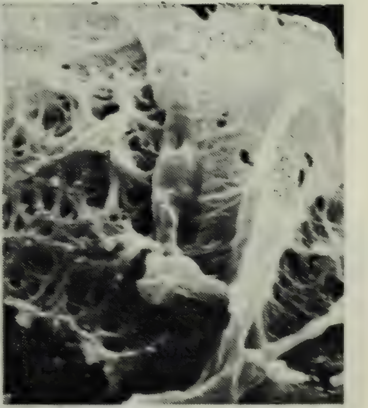

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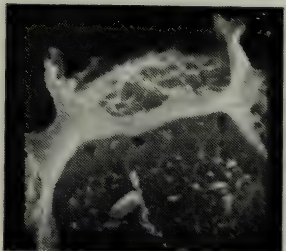

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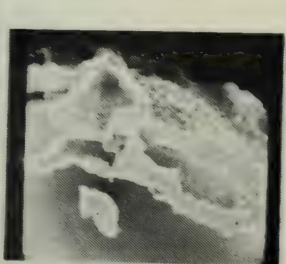

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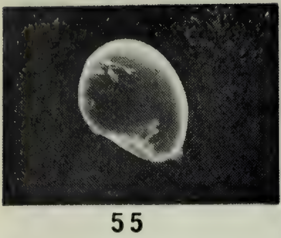
Plate V. Spore characteristics of *Arthropteris.*

Figs. *46*: Group of spores seen under low magnification; *47, 48*: normal spores and part of an ablated spore; *49, 50, 51, 52*: close-up views of the spores, showing detailed structures of various kinds of outgrowths on the perines; *53, 54*: broken spores, showing rough perines and smooth exines.

A. articulata: figs. *46* (x 250), *47* (x 750), *48* (x 750), *49* (x 2500); *A. pallisotii*: *50* (x 2500), *53* (x 750); *A. tenella*: *51* (x 2500); *A. beckleri*: *52* (x 1250); *A. dolichopoda*: *54* (x 1250).



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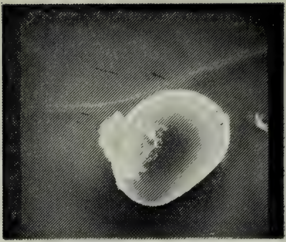

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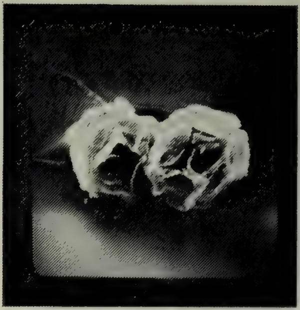

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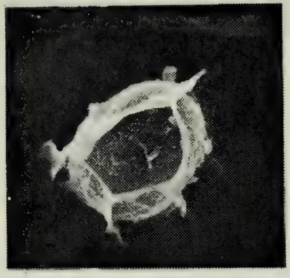

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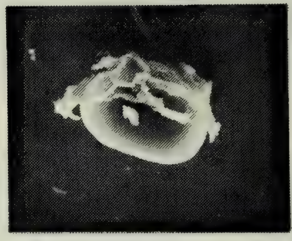

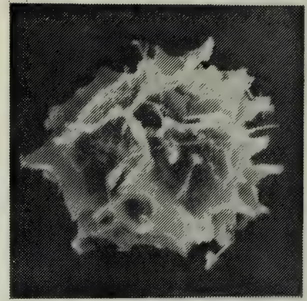

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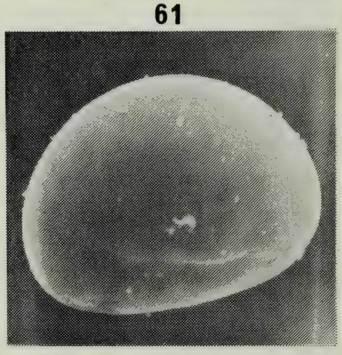

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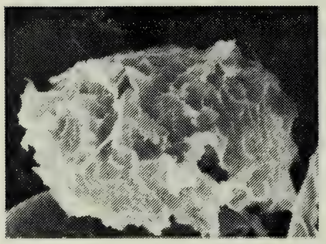

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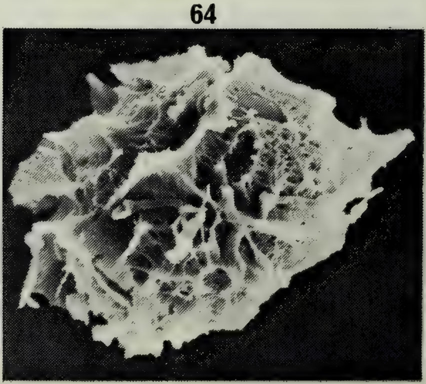

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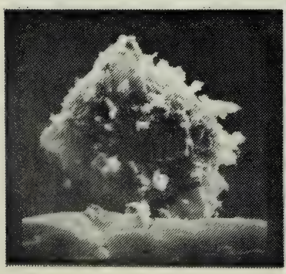

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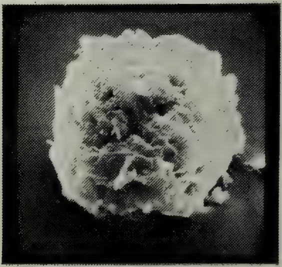

Plate VI. Some representative spores of *Arthropteris* species.

A. beckleri: figs. *55* (x 500), *56* (x 500); *A. dolichopoda*: *57* (x 500). *58* (x 500); *A. monocarpa*: *59* (x 250); *A. obliterata*: *60* (x 750); *A. pallisotii*: *61* (x 750), *62* (x 500); *A. repens*: *63* (x 500); *A. tenella*: *64* (x 1000); *A. wollastonii*: *65* (x 500), *66* (x 500).

SAURAUIAE GERONTOGEAE

I. Notes on Malayan species

by

R. D. Hoogland

Australian National University

Canberra

Abstract

Saurauia tristyla has been erroneously recorded from Malaya; the correct placement of these records is discussed. *S. roxburghii* Wall. and *S. napaulensis* DC. are new records for the area. *S. pentapetala* (Jack) Hoogl. is proposed as a new combination, with basionym *Ternstroemia pentapetala* Jack. Three new species are described: *S. fragrans* Hoogl., *S. mahmudii* Hoogl., and *S. malayana* Hoogl. *S. cauliflora var. calycina* King is placed in synonymy under *S. leprosa* Korth., and *S. grandis* Ridl. in synonymy under *S. vulcani* Korth. The altitudinal distribution of the 10 species found in Malaya is discussed.

Introduction

Under the general title SAURAUIAE GERONTOGEAE the author hopes to present a number of papers on the Old World species of *Saurauia*. The present must be seen only as one which is preliminary to a fully documented account of the Malayan species to be presented in the near future. Other accounts currently being prepared cover the species from continental South-East Asia, Java, and the Lesser Sunda Islands. Considering the high degree of local endemism in the genus, the preparation of separate treatments for the major islands or island groups of Malesia offers the opportunity to gradually compound our knowledge of the genus in this region.

The author is grateful to the authorities of the following herbaria for their cooperation in allowing the study of their collections during visits or by way of loans:

Botanical Section, Department of Agriculture, Bangkok (BK).
Forest Herbarium, Royal Forest Department, Bangkok (BKF).
British Museum (Natural History), London (BM).
Herbarium Bogoriense, Bogor (BO).
Central National Herbarium, Botanical Survey of India, Sibpore, Howrah (CAL).
Herbarium Australiense, C.S.I.R.O., Canberra (CANB).
Royal Botanic Garden, Edinburgh (E).
Conservatoire et Jardin botaniques, Genève (G).
Royal Botanic Gardens, Kew (K).
Forest Research Institute, Kepong (KEP).
Department of Botany, University of Malaya, Kuala Lumpur (KLU).
Rijksherbarium, Leiden (L).
Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris (P).
Botanic Gardens, Singapore (SING).
Botany Department, Universiti Kebangsaan Malaysia, Kuala Lumpur (UKM).

Fieldwork in Malaya was made possible with generous assistance from the University of Malaya, Kuala Lumpur; the Forest Research Institute, Kepong; the Universiti Kebangsaan Malaysia, Kuala Lumpur; and the Botanic Gardens, Penang.

I am indebted to Mrs. Cathy Porter for the illustrations of *Saurauia mahmudii* and *S. malayana,* and to Miss Jill Ruse for those of *S. fragrans.*

I. *Saurauia tristyla* auct. non DC. in Malaya

The type of *Saurauia tristyla* DC. [in Mem. Soc. Phys. Hist. Nat. Genève 1 (1822) 423, t. vii] originated from the Moluccas and represents a species which has subsequently been collected repeatedly there and in Celebes (Sulawesi). It has also been recorded from a wide geographical area including West New Guinea, Sumatra, Borneo, Malaya, Burma, Thailand, Indo-China, and Southern China (including Taiwan). Most, if not all, of these further records must be discarded as being referable to other species. The present note concerns itself only with the records and collections from Malaya and Peninsular Thailand. The main literature, under this name and for this area, is contained in King [in J. Asiat. Soc. Beng. 59 II (1890) 197], Ridley [Fl. Mal. Pen. 1 (1922) 207], Craib [Fl. Siam. Enum. 1 (1925) 129], and Keng [in Fl. Thail. 2 (1972) 110].

A study of the material in CAL, seen and annotated by King, revealed that he included specimens of three species for which I accept the names *Saurauia fragrans* Hoogl., *S. pentapetala* (Jack) Hoogl., and *S. roxburghii* Wall. In addition, two specimens which I refer to *S. pentapetala* were annotated *S. cauliflora* DC. (Scortechini 99) and *S. pendula* Bl. (Scortechini 331) whereas one collection (Scortechini s.n.: CAL 49323/4) of *S. roxburghii* was annotated "quite different from *S. tristyla* DC., G. King". None of these appear to have been considered further in King's account of the genus in the Materials for a Flora of the Malayan Peninsula. The same three species were available to Ridley in the herbaria of Singapore and Kew and included by him in *S. tristyla,* but as *S. fragrans* has not been found in Thailand the accounts of *S. tristyla* by Craib and Keng include only the other two species.

1. **Saurauia pentapetala** (Jack) Hoogl., *comb. nov.*

Basionym: *Ternstroemia pentapetala* Jack in Mal. Misc. 1 (5) (1821) 40; *cf.* Merr. in J. Arn. Arb. 33 (1952) 247. = *Cleyera pentapetala* (Jack) Spreng., Linn. Syst. Veg. (ed. 16) 2 (1825) 596. = *Scapha pinangiana* Choisy in Mém. Soc. Phys. Hist. Nat. Genève 14 (1855) 119, *nom. illeg.* — TYPE: "Native of Pulo Penang", lost; NEOTYPE: *Hoogland 12601,* SE. slope of Penang Hill, Penang, 8 April 1975, on forest edge at ca 420 m altitude, in CANB, duplicates being distributed to K, KEP, L, SING, US.

Synonym: *Saurauia nudiflora* var. *angustifolia* Craib, Fl. Siam. Enum. 1 (1925) 128. — TYPE: "PATTĀNĪ. Bāchaw, c. 600 m., by stream in evergreen forest, *Kerr,* 7196"; HOLOTYPE in ABD, *n.v.,* ISOTYPES in BK, BM, E, K.

Misapplied name: *Saurauia tristyla* auct. non DC.: Wall., Numer. List (1829) no. 1466 *et* Pl. Asiat. Rar. 2 (1831) 40; Dyer in Fl. Br. Ind. 1 (1874) 287, *p.p.;* King in J. Asiat. Soc. Beng. 59 II (1890) 197, *p.p.;* Ridl., Fl. Mal. Pen. 1 (1922) 207, *p.p.;* Craib, Fl. Siam. Enum. 1 (1925) 129, *p.p.;* Burk. & Henders., Gard. Bull. Straits Settl. 3 (1925) 349, *p.p.*; Henders., *ibid.* 4 (1928) 226, *p.p.;* Burk., Dict. Econ. Prod. Mal. Pen. (1935) 1967 *et* ed. 2 (1966) 2002, *p.p.;* Keng in Fl. Thail. 2 (1972) 110, *p.p.*

The two earliest names, validly published for Old World species of *Saurauia,* are those given by W. Jack under the generic name *Ternstroemia* to one Sumatran and one Malayan species. The Sumatran species was correctly renamed *Saurauia rubiginosa* (Jack) Merr., but the required new combination has never been proposed for the Malayan species. The first author to have placed it in *Saurauia* appears to have been Dyer (1874) who lists it in synonymy under *S. tristyla* DC. This species had already been recorded from Penang, the type area for Jack's name, by Wallich (1829, 1831) on the basis of a specimen collected by Porter. All subsequent authors followed this placement of the name. Merrill, in his account of William Jack's genera and species of Malayan plants (1952), did not specifically place it beyond saying that it "belongs clearly in the group with *S. tristyla* DC."

Saurauia pentapetala is probably the most common and most widely distributed species in Malaya, having been found in most of the mainland states and on Penang and Singapore islands. In Peninsular Thailand it is known from Ranong and Surat Thani districts southward. The species is most commonly found in the lowlands, up to ca 500 m altitude, with an occasional occurrence at higher altitudes (up to 1100 m).

2. **Saurauia roxburghii** Wall., Numer. List. (1829) no. 1467, *nom. nud., et* Pl. Asiat. Rar. 2 (1831) 40. — TYPE from India.

Misapplied name: *Saurauia tristyla* auct. non. DC.: King in J. Asiat. Soc. Beng. 59 II (1890), 197, *p.p.*; Ridl. in Trans. Linn. Soc. London II Bot. 3 (1893) 277, *et* Fl. Mal. Pen. 1 (1922) 207, *p.p.*; Craib, Fl. Siam. Enum. 1 (1925) 129, *p.p.*; Burk. & Henders., Gard. Bull. Straits Settl. 3 (1925) 349, *p.p.*; Henders., *ibid.* 4 (1928) 226, *p.p.*; Burk., Dict. Econ. Prod. Mal. Pen. (1935) 1967 *et* ed. 2 (1966) 2002, *p.p.*; Keng in Fl. Thail. 2 (1972) 110, *p.p.*

Saurauia roxburghii is a widespread species of continental South-East Asia, extending from eastern Nepal through southern China to the Ryukyu Islands, through Burma, Thailand, and Indo-China, and is now for the first time recorded for Malaya. Here it is less widespread than *S. pentapetala*, being absent from Malacca, Johore, Singapore, and Penang, and, though it has been found at quite low altitudes, tends to be more frequent between 500 and 1000 m where it may be common in regrowth vegetation; the maximum recorded altitude is 1250 m.

3. **Saurauia fragrans** Hoogl., *sp. nov.* (fig. 2)

Arbor parva usque 12 m alta, 20 cm diametro. Folia oblonga vel obovato-oblonga, plerumque 18–30 cm longa, 6–11 cm lata, 14–17-nervata, apice acuta ± acuminata, basi acuta vel obtusa, petiolo 2–4 cm longo. Flores solitarii vel usque 20 fasciculati, interdum inflorescentia cymosa pauciflora interspersa, in axillis foliorum vel cicatricium foliorum. Pedunculus usque 5 mm longus, pedicellus 8–22 mm longus. Sepala suborbicularia, 3–5 mm longa et lata. Corolla late campanulata (fere plana), 2 mm alta, 13 mm diametro; tubus 1½–2 mm longus; lobi 5½–8½ mm longi, 4½–7½ mm lati, apice bilobulati. Stamina plerumque 20–23, filamentis subaequalibus 2½–3½ mm longis, antheris versatilibus dorsifixis 1½–2 mm longis. Ovarium subglobosum, 1.8–2.3 mm altum, 1.8–2.7 mm diametro, dense sericeo-hirsutum, triloculare; styli 3–4½ mm longi, basi ½ mm connati.

Squamae triangulares usque 0.7 mm longae, 0.3 mm latae, apice acuminatae, superficie dense trichomatosae, in ramellis, penndunculis, pedicellis, et foliis, praesertim facie inferiori; inter squamas pili crassiusculi usque 0.3 mm longi, frequenter stellatim collocati.

TYPE: *Hoogland 12571*, along Kuala Lumpur—Raub road between m.s. 53 and 54 (i.e. near The Gap), Selangor, 27 March 1975, in fairly tall secondary forest on roadside at ca 720 m altitude. HOLOTYPE in CANB, ISOTYPES being distributed to A, BO, E, G, K, KEP, L, MEL, SING, US.

Further collections examined: *Whitmore FRI 2622* (L, SING), *Kasim & Rahim K 750* (UKM), *Kunstler 10638* (CAL, K), *Teo & Pachiapa 340 = KL 2904* (K, L, SING), *Lye L 68/71* (SING), *Poore 856* (KLU), *Burkill SF 3184* (SING), *Stone 6894* (KLU).

Misapplied name: Saurauia tristyla auct. non DC.: King in J. Asiat Soc. Beng. 59 II (1890) 197, *p.p.:* Ridl., Fl. Mal. Pen. 1 (1922) 207, *p.p.;* Burk., Dict. Econ. Prod. Mal. Pen. (1935) 1967 *et* ed. 2 (1966) 2002, *p.p.*

Saurauia fragrans is known only from a few localities in Selangor: The Gap (straddling the Selangor—Pahang boundary), Kepong, Ulu Bubong, and Ulu Gombak, and one in Negri Sembilan: Gunong Tampir, occurring at elevations from 75 to 750 m. Outside Malaya it has also been found in Northern Sumatra.

The specific epithet has been chosen as, in contrast with other species of *Saurauia* encountered by me in India, Malaya, Java, Flores and New Guinea, the flowers of the type specimen were heavily sweet-scented, a feature made even more noticeable because of the very large number of flowers present on the tree. The fragrance of the flowers was also noted in *Lye L 68/71.*

The differences between *Saurauia roxburghii, S. pentapetala,* and *S. fragans* are set out in the accompanying table.

S. roxburghii	*S. pentapetala*	*S. fragrans*
	INFLORESCENCE	
(1-) 3-7-flowered, often open with relatively long peduncle; at least those below the leaves in cluster of up to 4.	1-3 (-5)-flowered, in most plants predominantly 1-flowered, with at most short peduncle; at least those below the leaves in cluster of up to 15.	1 (-3)-flowered, with at most short peduncle; at least those below the leaves in cluster of up to 20.
	PEDUNCLE AND PEDICELS	
With tomentum of very short villose hairs and occasionally a few small elongated scales.	With broad-based scales, with villose tomentum incorporated in base of scales and sparse or mostly absent between scales.	With long fairly broad based scales and short trichomes on base of and between scales.

SEPALS		
Outer ones in length about 2/3 of inner ones, ca 2.6-4.0 resp. 3.8-5.2 mm long, at least where exposed in bud with some short villose tomentum outside. Hardly enlarged in fruit, appressed to and distinctly shorter than mature fruiting ovary.	Outer and inner sepals similar in length, ca 5-8 mm long; glabrous outside. Distinctly enlarged to 1½-2 times original size in fruit, similar in length to fruiting ovary, in upper part usually curved away from fruiting ovary.	Outer and inner sepals similar in lenth, ca 3-5 mm long; at least where exposed in bud finely stellate-tomentose outside. Fruiting calyx unknown.
COROLLA		
Tube urceolate, about ½ of total length of corolla (which is ca 6-7 mm). Lobes usually rounded, rarely with shallow incision in middle at apex, in bud of varying aestivation, rarely contort.	Tube broad-campanulate, only about ¼ or less of total length of corolla (which is ca 8-15 mm). Lobes with shallow incision in middle of apex, always of contort aestivation in bud.	Tube broad-campanulate, only about ¼ or less of total length of corolla (which is ca 7-10 mm). Lobes with shallow incision in middle of apex, always of contort aestivation in bud.
STAMENS		
34-47 Filaments with several long hairs, mainly in lower part. Anthers basifixed, not versatile, at most retuse at apex.	28-44 Filaments glabrous. Anthers dorsifixed, versatile, bifid at apex.	18-26 Filaments glabrous. Anthers dorsifixed, versatile, bifid at apex.
OVARY		
Glabrous. 3-5-locular. Style arms spreading horizontally from early bud stage to in open flower. Ovule number ca 80-120 per cell. Mature fruiting ovary ca 6 mm diam. and tall.	Glabrous. 3-4 (-5)-locular. Style arms contort in early bud to erect and straight in nearly open flower, only slightly spreading in open flower. Ovule number ca 300-350 per cell. Mature fruiting ovary ca 11 mm diam., ca 7½ mm tall.	Densely hirsute (hairs up to 0.5 mm long). (2-) 3 (-4)-locular. Style arms contort in early bud to erect and straight in nearly open flower, slightly spreading in open flower. Ovule number ca 240-260 per cell. Mature fruiting ovary unknown.

II. *Saurauia* in the Cameron Highlands

During a short visit to the Cameron Highlands in May 1973 I was able to collect a number of specimens of *Saurauia*. On closer examination it became clear that amongst these collections two undescribed species were represented. When I revisited the area in March-April 1975, I took the opportunity of collecting further specimens of these two species and making notes of their altitudinal occurrence. Similarly, the altitudinal zonation of the other species in the area and along the access road from Tapah to Tanah Rata was noted and in part documented by the collecting of herbarium specimens. It appeared that out of ten species now known to occur in Malaya, eight are found in the area covered. Only *S. rubens* Ridl. and *S. fragrans* Hoogl., both of limited known occurrence, are absent.

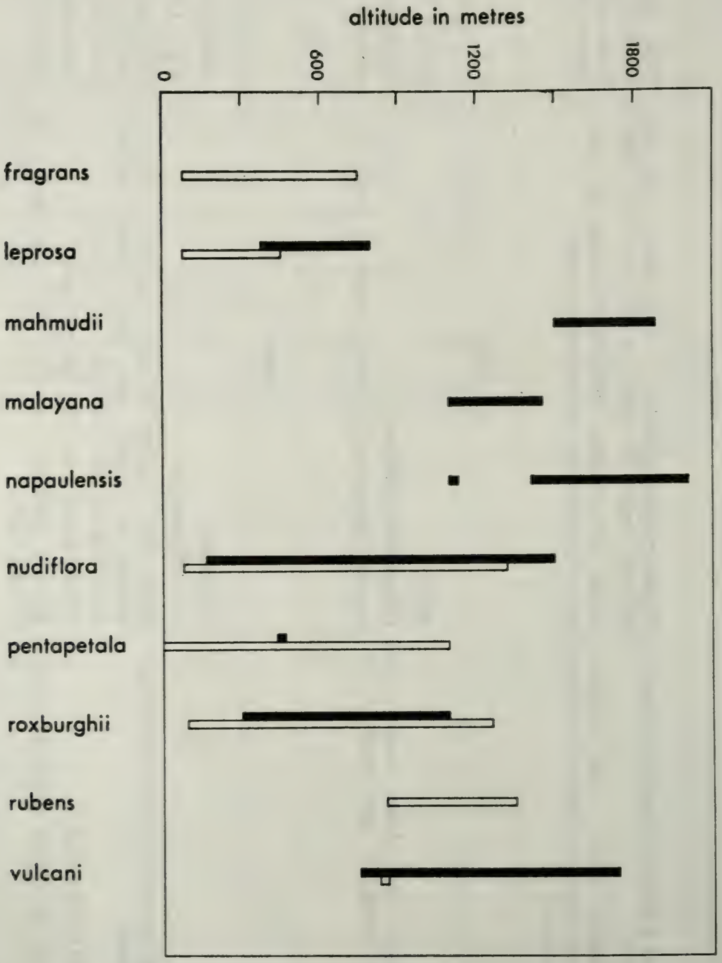

Fig. 1. Known altitudinal range of *Saurauia* species in the Cameron Highlands (solid block) and elsewhere in Malaya (open block).

In fig. 1 the observed altitudinal range in the Cameron Highlands and along the road from Tapah is presented along the altitudinal range outside the Cameron Highlands of all species known from Malaya as ascertained from data available of herbarium specimens. The species are arranged in alphabetical order; apart from those already treated the following are involved:

Fig. 2. *Saurauia fragrans* Hoogl. *a.* flowering branch, × $\frac{2}{5}$; *b.* and *c.* open flower, × 2; *d.* flower bud just before opening, × 3; *e.* longitudinal section of flower, × 2; *f.* stamens, × 4. All after *Hoogland 12571*.

4. **Saurauia leprosa** Korth., Verh. Nat. Gesch. Kruidk. (1842) 131. — TYPE from Java.

Synonym: *Saurauia cauliflora* var. *calycina* King in J. Asiat. Soc. Beng. 59 II (1890) 199; Ridl., Fl. Mal. Pen. 1 (1922) 208; Craib, Fl. Siam. Enum. 1 (1925) 127; Henders. in J. Mal. Br. Roy. Asiat. Soc. 17 (1939) 25, 37; Keng in Fl. Thail. 2 (1972) 110. — TYPE: "Perak: Batu Kurau. Scortechini, No. 1614."; HOLOTYPE in CAL, ISOTYPE in SING.

Misapplied name: *Saurauia cauliflora* auct. non DC.: Burk. & Henders. in Gard. Bull. Straits Settl. 3 (1925) 336, 349; Henders. *ibid.* 4 (1928) 226; Burk., Dict. Econ. Prod. Mal. Pen. (1935) 1967 *et* ed. 2 (1966) 2002.

This is in Malaya a rather rare mainly lowland species found only in Perak, Pahang, and Selangor, and occurs outside Malaya in Peninsular Thailand, Sumatra, and Java. Throughout its range some individuals are almost exclusively cauliflorous, others are exclusively ramiflorous or carry the inflorescences in the leaf axils, while few individuals show the whole range of inflorescence positions.

5. **Saurauia mahmudii** Hoogl., *sp. nov.* (fig. 3)

Arbor parva usque 6 m alta. Folia obovata vel obovato-oblonga, plerumque 20–30 cm longa, 10–15 cm lata, 20–28-nervata, apice obtusa late acuminata, basi acuta subdecurrentia, petiolo 2½–4½ cm longo. Inflorescentiae solitariae vel 2–4 fasciculatae in axillis foliorum vel cicatricium foliorum, pro parte majori dichasia triflora, nonullae biflorae vel uniflorae, usque 7 cm longae. Pedicellus 2–5 cm longus. Sepala 9–12 mm longa, 8–10 mm lata, basi 3 mm crassa. Corolla late urceolata, 13–15 mm longa, 15 mm diametro; tubus 7–9 mm longus, 12 mm diametro; lobi 8–10 mm longi, 7½–11 mm lati, recurvati, apice bilobulati. Stamina plerumque 25-32, filamentis subaequalibus 5–5½ mm longis, antheris versatilibus dorsifixis 2½–3 mm longis. Ovarium semi-globosum 3–3½ mm altum, 5 mm diametro, glabrum, triloculare; styli 7 mm longi, basi 1½–2 mm connati.

Squamae anguste triangulares, 0.5–1.0 mm longae, 0.2–0.3 mm latae, acutae, margine praesertim inferiori piloso. In ramis, foliis, pedunculis, pedicellis, bracteis, et bracteolis sparsae; in sepalis absunt, interdum uno vel duabus basi exceptis.

TYPE: *Hoogland 12579,* along road to summit of Gunong Brinchang near m.s. 46, Cameron Highlands, Pahang, 1 April 1975, in gully on steep slope at ca 1770m altitude. HOLOTYPE in CANB, ISOTYPES being distributed to BRI, K, KLU, L, SING, US.

Further collections examined: *Whitmore FRI 15449* (KEP), *Hoogland 12326* (CANB, K, KEP, L), *12327* (CANB, SING), *12328* (CANB, SING). *12580* (CANB. L), *12581* (A, BO, CANB, KEP), *Kasim & Zainudin K 988* (UKM), *Stone 5595* (KLU); all from the Gunong Brinchang area.

The species closely resembles *S. nudiflora* from which it is readily distinguished by the glabrous ovary as against densely sericeous. In *S. nudiflora* nearly all flowers are solitary though a few 2- or 3-flowered inflorescences occur in most plants; in *S. mahmudii* the inflorescences are mostly 3-flowered with fewer 2- or 1-flowered ones interspersed. Individuals with predominantly 3-locular ovaries are found in *S. nudiflora,* though only one such collection is known to me (*Hoogland 12570*) in which the flowers are smaller, with a smaller than usual number of stamens for this species. In all other collections examined the ovary is predominantly 5-celled, with occasional flowers with 4- or 6-celled ovary. Var. *tetragyna* Boerl., originating in Java, is reported to have a 4-celled ovary. In all collections of *S. mahmudii* the ovary is 3-celled (one 2-celled ovary was found in 130 flowers analysed).

I have dedicated this species to Mahmud bin Sider, of the University of Malaya, who assisted me in collecting in the Cameron Highlands in 1973 and 1975.

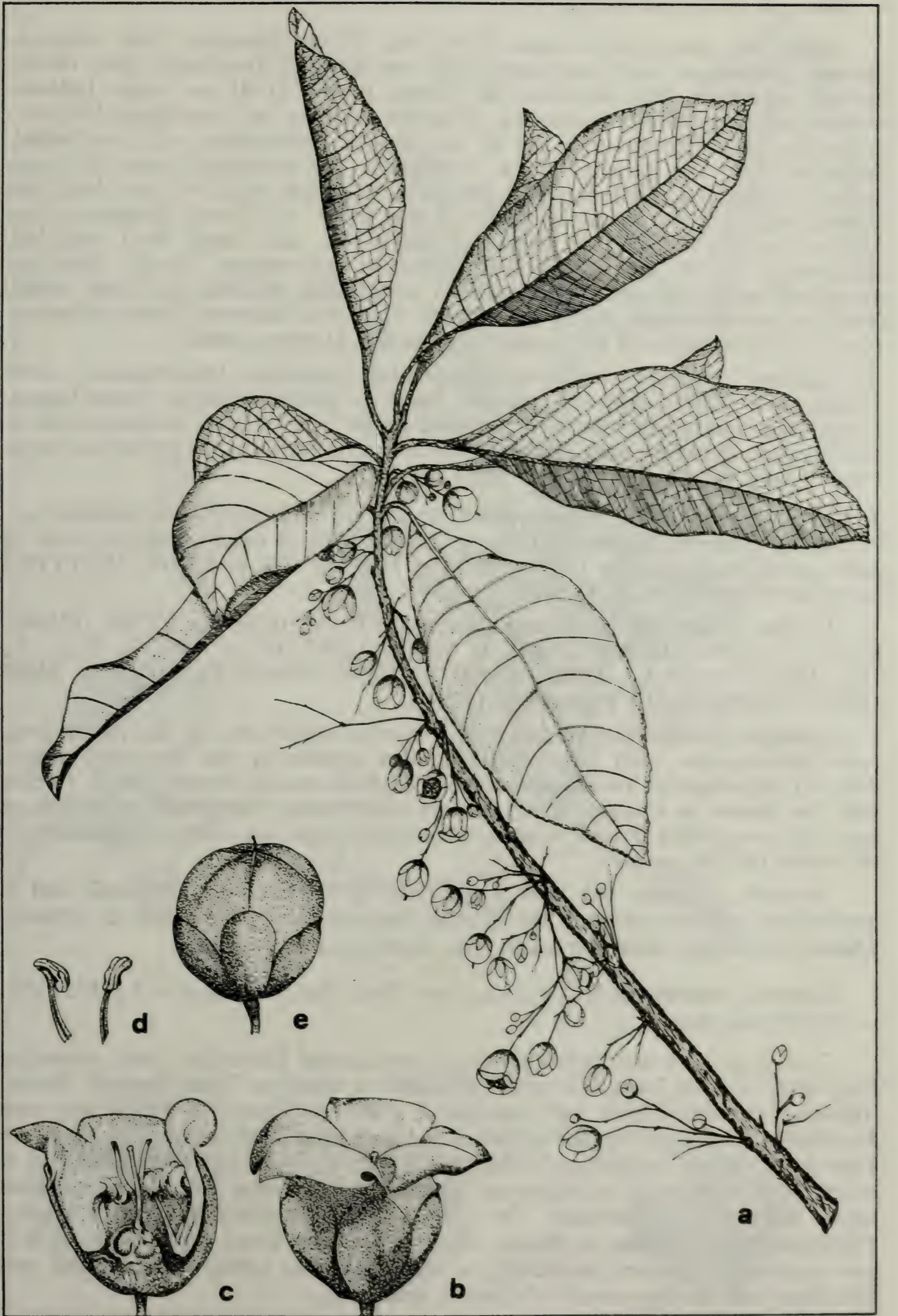

Fig. 3. *Saurauia mahmudii* Hoogl. *a.* flowering branch, × ½; *b.* open flower, × 2; *c.* longitudinal section of flower, × 2; *d.* stamens, × 2; *e.* fruit, × 2. All after *Hoogland 12579.*

6. **Saurauia malayana** Hoogl., *sp. nov.* (fig. 4)

Frutex vel arbor parva usque 12 m alta, 20 cm diametro. Folia obovato-oblonga, plerumque 14–32 cm longa, 6–15 cm lata, 12–20-nervata, apice obtusa breviter acuminata, basi rotundata vel obtusa, petiolo 1½–4½ cm longo. Inflorescentiae solitariae vel 2–3 fasciculatae in axillis foliorum vel cicatricium foliorum, dichasiales, 3–20-florae, usque ad 20 cm longae. Pedunculus 1–10 cm longus. Pedicellus 5–40 mm longus. Sepala 2 exteriora late triangulari-ovata, 8–9 mm longa, 9–12 mm lata; 2 interiora suborbicularia, 8–10 mm longa, 9–12 mm lata; basi 2 mm crassa. Corolla campanulata, 10–15 mm longa, 16–20 mm diametro; tubus 5–7 mm longus, 10–13 mm diametro; lobi 8½–11 mm longi, 9–13 mm lati, aliquantum reflexi, apice bilobulati. Stamina plerumque 30–40, filamentis subaequalibus 3½–5½ mm longis, antheris versatilibus dorsifixis 2–3 mm longis. Ovarium semi-globosum 2½–3½ mm altum, 4½–6 mm diametro, dense hirsutum, (4-) 5 (-7)-loculare; styli 5½–7½ mm longi, basi 1–2½ mm connati.

Squamae anguste triangulares acuminatae, superficie trichomatosae; inter squamas pili graciles stellatim collocati. Squamae ramorum usque 4 mm longae, 1 mm latae (plerumque minores), foliorum usque 3 mm longae, pedunculorum et pedicellorum usque 1½ mm longae, faciei exterioris sepalorum exteriorium usque 1 mm longae. Pili graciles usque 1 mm longi.

TYPE: *Hoogland 12591*, along road from Ringlet to Tanah Rata between m.s. 29 and 30, Cameron Highlands, Pahang, 2 April 1975, in open secondary forest in gully on steep slope at ca 1150 m altitude. HOLOTYPE in CANB, ISOTYPES being distributed to A, G, K, KEP, L, SING, US.

Further collections examined: *Hoogland 12332* (CANB), *12335* (CANB, KLU, L), *12576* (A, BO, CANB, E, KEP), *12586* (BO, CANB, E, KLU, L, US), *12587* (CANB, L), *12588* (CANB, L), *12590* (CANB, G, K, SING), *12595* (BH, E, CANB, KLU), *Turnau 789* (KLU).

Amongst its Malayan congeners this species stands out by the rather long, open inflorescences with large flowers. Other species in the area with many-flowered inflorescences are *S. napaulensis* with much smaller flowers and *S. vulcani* with the flowers in a much more compact inflorescence. Both these species have generally many more flowers to each inflorescence, and also differ substantially in the nature of their scales.

Saurauia malayana has been found only in the Cameron Highlands and is particularly common around the Ringlet between 1100 and 1300 m altitude, whereas a few trees were also found near Tanah Rata at 1400 m.

7. **Saurauia napaulensis** DC. in Mém. Soc. Phys. Hist. Nat. Genève 1 (1822) 421. — TYPE from Nepal.

This is another widespread species of continental South-East Asia, extending from north-western India (Himachal Pradesh) to southern China, through Burma, Thailand, and Indo-China, and now, like *S. roxburghii*, recorded for the first time for Malaya. Compared to that species, it ranges further West in the foothills of the Himalayas, but not as far East in the Chinese region. While I have no hesitation in accepting *S. roxburghii* as indigenous in Malaya, there must be some reservations about this for *S. napaulensis*. The species was not collected in the Cameron Highlands (the only area in Malaya where it has been found until 1936) but it is now extremely common, particularly in disturbed areas between Tanah Rata and Brinchang and on the summit of Gunong Brinchang.

The species is grown as an ornamental in the tea-growing areas of Ceylon and, in particular, of Southern India and the possibility of its introduction into the Cameron Highlands for the same purpose cannot be discarded. On the other hand,

Fig. 4. *Sauranuia malayana* Hoogl. *a.* flowering branch, × ½; *b.* open flower, × 2; *c.* longitudinal section of flower, × 2; *d.* stamens, × 2; *e.* imature fruit, × 2. All after *Hoogland 12591.*

it may have occurred there naturally and extended its area substantially with the opening up of the highland country. The nearest known natural occurrences outside Malaya are in Thailand on Doi Inthanon in Chieng Mai district and Phu Miang in Phitsanulok district, some 1500 km to the North.

8. **Saurauia nudiflora** DC. in Mém. Soc. Phys. Hist. Nat. Genève 1 (1822) 422, t. v; King in J. Asiat. Soc. Beng. 59 II (1890) 198; Ridl. in Trans. Linn. Soc. London II Bot. 3 (1893) 277, in J. Fed. Mal. St. Mus. 4 (1909) 6, *et* Fl. Mal. Pen. 1 (1922) 207; Burk. & Henders. in Gard. Bull. Straits Settl. 3 (1925) 336, 349; Henders., *ibid.* 4 (1928) 226; Burk., Dict. Econ. Prod. Mal. Pen. (1935) 1967 *et* ed. 2 (1966) 2002. — TYPE from Java.

Common in north-western Malaya, where it has been found in Kedah, Perak, Pahang, and Selangor. Outside Malaya it occurs in Sumatra and Java.

9. **Saurauia rubens** Ridl. in J. Roy. Asiat. Soc. Straits Br. 61 (1912) 1, et Fl. Mal. Pen. 1 (1922) 208. — TYPE: "Selangor: Semangkok Pass, at the foot of the hill leading to the Sempang mines."; HOLOTYPE in SING (*Ridley 15771*, "Sempang track, Ap. 1911"), ISOTYPE in BM.

Common in the Fraser's Hill area, also collected once in Trengganu (Mandi Angin). Endemic to Malaya.

10. **Saurauia vulcani** Korth., Verh. Nat. Gesch. Kruidk. (1842) 128. — TYPE from Sumatra.

Synonym: *Saurauia grandis* Ridl. in J. Fed. Mal. St. Mus. 4 (1909) 6 *et* Fl. Mal. Pen. 1 (1922) 207. — TYPE: "Telôm River banks."; HOLOTYPE in SING (*Ridley 13580*, "Telom, Nov. 1908"), ISOTYPES in BM, K.

Apart from its abundant occurrence in the Cameron Highlands, this species is known from Malaya only from a recent collection from the Genting Highlands. It spreads readily on disturbed roadsides and on landslides.

The Cyperaceae Tribe Cypereae of Ceylon

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Abstract

This taxonomic treatment, revising all the Ceylonese taxa of the Cyperaceae tribe Cypereae, enumerates 59 species of four genera, *Cyperus, Pycreus, Mariscus* and *Kyllinga.* The following new names are proposed: *Cyperus compressus* ssp. *micranthus, C. diffusus* ssp. *macrostachyus, C. nutans* ssp. *eleusinoides, Pycreus flavidus, P. pumilus* ssp. *membranaceus, Mariscus cyperinus* ssp. *laxatus, M. pedunculatus, M. sumatrensis,* and *Kyllinga odorata* ssp. *cylindrica.*

In the course of my preparation of a taxonomic account of the Cyperaceae for the Flora of Ceylon, a project under the auspices of the Smithsonian Institution (Koyama 1970), I have had the opportunity of revising important historical collections of Ceylonese Cyperaceae that are housed in the Herbarium of the National Botanic Gardens, Peradeniya. These old collections, of which only a part is represented at Kew and elsewhere, have not received the attention of specialists since Trimen published his Handbook (1900). In addition, a series of field expeditions recently sent to Ceylon (Koyama 1970, 1974) resulted in an accumulation of a substantial number of critical gatherings, among which are several cyperoid taxa that are new to the flora of Ceylon. In the present paper 59 species of the tribe Cypereae are recognized as valid for the flora of Ceylon and are classified under four genera, *Cyperus, Pycreus, Mariscus* and *Kyllinga.* The treatment not only identifies the collections mentioned above but also updates the nomenclature with particular emphasis on the coordination to the two recent imporant works on the Cypereae (Kükenthal 1935-36; Kern 1974). The remarkable richness of cyperoid taxa in Ceylon rests on the fact that besides the so-called Indo-Malesian and the Pantropic elements, on this little island there occur Western Asiatic elements reaching Ceylon as well as those interesting endemic ones which are confined to the southern part of Deccan Peninsula and Ceylon. Special attention was paid to these entities of phytogeographic interest.

I appreciate the assistance of Dr. F.. Raymond Fosberg, who has given me this opportunity of studying Ceylonese Cyperaceae. Messrs R. Cooray, T. Herat, N. Balakrishnan, A. H. M. Jayasuria and K. Sumithraarachchi certainly deserve my sincere thanks for their help in the field. The financial assistance from the Smithsonian Office of International Program is gratefully acknowledged for their research grant in defraying my field expenses.

KEY TO GENERA

1. Rhachilla not articulated, persistent, hence glumes falling apart from rhachilla
    2. Achenes triquetrous or dorsi-ventrally flattened with one side facing rhachilla .... *Cyperus*
    2. Achenes laterally flattened with one angle facing rhachilla .... *Pycreus*
1. Rhachilla articulated, hence spikelets falling in entirety
    3. Achenes triquetrous with one side facing rhachilla .... *Mariscus*
    3. Achenes laterally flattened with one angle facing rhachilla .... *Kyllinga*

CYPERUS L.

1. Stigmas 3, or style more or less undivided (sp. no. 33)
2. Spikelets spicately disposed on conspicuously elongated rhachis, thus forming spikes
3. Rhachilla of spikelets winged with base of glumes, which is decurrent along the rhachilla internode
4. Spikelets many to numerous; spikes with long rhachis, cylindrical, normally 3–7 cm long
5. Leaves with elongated blade
6. Spikelets linear, terete or subterete, 0.5–1 mm wide
7. Spikelets patent to spreading; spikes as a rule peduncled; leaves 4–15 mm wide; culm smooth on angles .... **1** *C. digitatus*
7. Spikelets erect to suberect; spikes subfastigiate, subsessile; leaves 20–30 mm wide; culms scabrous on upper angles .... **2** *C. platyphyllus*
6. Spikelets lanceolate to lance-oblong, *ca.* 1.5 mm wide, flattened .... **3** *C. exaltatus*
5. Leaves reduced to bladeless sheaths .... **4** *C. papyrus*
4. Spikelets several to teens, occasionally up to 30; spikes with rather short rhachis broadly ellipsoid or ovoid, normally 1–4 cm long
8. Plants with creeping rhizomes or stolons (except in *C. bulbosus*, which bears tunicate bulb at base of culm)
9. Culms thick, normally more than 5 mm wide and 60 cm tall, clothed at base with bladeless sheaths
10. Culms obtusely trigonous to subterete; glumes lance-ovate, acute-tipped; bracts much shorter than corymb
11. Culms not septate .... **5** *C. corymbosus*
11. Culms transversely septate ...... **6** *C. articulatus*
10. Culms acutely triquetrous; glumes oblong, obtuse at apex; bracts much surpassing corymb .... **7** *C. pangorei*
9. Culms slender, mostly 1–2 mm wide and less than 60 cm tall; leaves with elongated blade
12. Culms arising from bulbose base, tufted .... **8** *C. bulbosus*
12. Stolons present; culm bases forming a corm-like enlargement
13. Glumes 2–2.5 mm long; spikelets slightly swollen; leaves normally as long as the culm .... **9** *C. stoloniferus*
13. Glumes 3–4 mm long; spikelets strongly flattened; leaves normally much shorter than the culm
14. Culms 10–30 cm tall; bracts as long as or shorter than the inflorescence .... **10** *C. rotundus*
14. Culms 30–60 cm tall; bracts 2 to 3 times as long as the inflorescence

15. Spikelets linear-lanceolate, gradually narrowed to an acute apex, 2.2–3 mm wide; glumes ovate

16. Glumes 3–3.5 mm long, red-brown, close together not exposing achene between two glumes; spikelets 2.2–2.5 mm wide .... **11** *C. tuberosus*

16. Glumes 4 mm long, yellow-brown, slightly spaced exposing portion of achene between two glumes; spikelets 3–3.2 mm wide .... **12** *C. retzii*

15. Spikelets linear, rather suddenly obtusish at apex, 1.5–2 mm wide glumes oblong .... **13** *C. scariosus*

8. Plants without creeping rhizomes or stolons

17. Spikelets linear to lanceolate, 1.5–2 mm wide; weakly flattened with two acute edges; glumes close together, acute at apex

18. Glumes distinctly colored with red-brown, brown or dark brown; plants perennial with culms more or less enlarged at base

19. Glumes 2.2–2.5 mm long, pale-green and strongly colored with dark or purple-brown .... **14** *C. sphacelatus*

19. Glumes 3–3.5 mm long, straw-colored and tinged with reddish brown or brown .... **15** *C. tenuiculmis*

18. Glumes pale or stramineous-green, not at all brown-colored; plants annual with fibrous roots only; culms not thickened at base .... **16** *C. zollingeri*

17. Spikelets filiform, subterete, less than 1 mm thick; glumes spaced, obtuse at apex

20. Spikelets spreading, ca. 0.75 mm wide; glumes rounded-obtuse at apex with moderately narrow hyaline margins .... **17** *C. distans*

20. Spikelets erect-patent, ca. 1 mm wide; glumes shallowly emarginate at apex with very broad hyaline margins .... **18** *C. nutans*

3. Rhachilla of spikelets without conspicuous wings, base of glumes not decurrent along the rhachilla internode

21. Plants perennial with stolons

22. Rhachis of spikes glabrous; glumes obtuse at white-hyaline apex .... **19** *C. procerus*

22. Rhachis of spikes densely hispid; glumes acute at apex without broad hyaline apex .... **20** *C. pilosus*

21. Plants annual, with fibrous roots only

23. Spikelets 1–2.5 cm long, 2–3 mm wide; glumes 2–3.5 mm long, acute at apex, tightly disposed

24. Glumes 3.5 mm long; achenes 1.5 mm long; inflorescence usually open with elongated rays .... **21b** *C. compressus* ssp. *compressus*

24. Glumes 2 mm long; achenes 1 mm long; inflorescence congested in a head-like cluster .... **21b** *C. compressus* ssp. *micranthus*

23. Spikelets 0.5–1 cm long, 1–1.5 mm wide; glumes 0.75–1.25 mm long, obtuse at apex, loosely disposed .... **22** *C. iria*

2. Spikelets digitately disposed or capitately congested at apices of inflorescence rays, thus forming heads without rhachis

25. Inflorescences open with elongated rays

26. Large-sized perennials with conspicuous rhizome; at least some leaves and bracts more than 10 mm wide; culms 30–90 cm tall

27. Leaves with elongated blade; leafy bracts 5–10

28. Achenes with acute angles; spikelets in clusters of 2 or 3, sometimes solitary, weakly compressed

28a. Spikelets 4–6 mm long, up to 12-flowered .... **23a** *C. diffusus* ssp. *diffusus*

28a. Spikelets 10–20 mm long, up to 40-flowered .... **23b** *C. diffusus* ssp. *macrostachyus.*

28. Angles of achenes spongy-thickened; spikelets in clusters of 5 to 8, strongly compressed .... **24** *C. platystylis*

27. Leaves reduced to bladeless sheaths, leafy bracts more than 15 .... **25** *C. alternifolius* ssp. *flabelliformis*

26. Small to medium-sized annuals or short-lived perennials; leaves and bracts at most 5 mm wide; culms up to 40 cm tall

29. Umbel rays longer than or nearly as long as the culm .... **26** *C. radians*

29. Umbel rays much shorter than the culm

30. Glumes awnless; achenes obovate; leaves flattish

31. Spikelets digitate in clusters of 3–15; glumes acutish at apex

32. Roots brownish; basal sheaths straw-brown or pale-brown; spikelets dark green .... **27** *C. pulcherrimus*

32. Roots purplish; basal sheaths purple-brown; spikelets brown or purple-brown

33. Glumes densely imbricate and close together so that achenes not shown between glumes; rhizome often conspicuous, rather frequently elongated .... **28** *C. haspan*

33. Glumes sublaxly imbricate and slightly spaced, thus achenes exposed between glumes; plants tufted with fibrous roots only .... **29** *C. tenuispica*

31. Spikelets many, congested in globose heads .... **30** *C. difformis*

30. Glumes awned at apex; achenes oblong; leaves canaliculate

34. Glumes with straight awn ...... **31** *C. castaneus*

34. Glumes with recurved awn ...... **32** *C. cuspidatus*

25. Inflorescences congested a single head

35. Style 3-cleft; achenes acute on angles

36. Rhizome with long creeping stolons; culms 5–20 cm tall; heads 1–2 cm wide .... **33** *C. arenarius*

36. Rhizome short, culms tufted, 20–60 cm tall; heads more than 3 cm across .... **34** *C. conglomeratus*

35. Style scarsely divided at apex; achenes with spongy-thickened angles; plants floating on water .... **35** *C. cephalotes*

1. Stigmas 2

37. Tall perennial; culms ca. 100 cm tall; inflorescences umbelliform with elongated rays up to 18 cm long .... **36** *C. alopecuroides*

37. Small annual; culms 5–18 cm tall; inflorescence a head .... **37** *C. pygmaeus*

1. **Cyperus digitatus** Roxburgh, [Hort. Beng. 81, 1814, nomen, &] Fl. Indica ed. 1, **1**: 209, 1820; C. B. Clarke, Fl. Brit. India **6**: 618, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 36, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 55, 1935; Kern, Fl. Males. I, **7** (3): 601, 1974.

'*Cyperus venustus* R. Br.' *sensu* Nees, Contrib. Bot. India 86, 1834. —— '*Cyperus neesii* Kunth' *sensu* Thwaites, Enum. Pl. Zeyl. 344, 1868. —— *Cyperus hookeri* Böckeler, Linnaea **36**: 308, 1870. —— *Cyperus digitatus* Roxb. var. *hookeri* (Böcklr.) C. B. Clarke, Fl. Brit. India **6**: 618, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 37, 1900.

Jaffna District: *Ca.* 5 miles W of Paranthan, south shore of Jaffna Lagoon, *T. Koyama et al. 14043* (NY, PDA, US); Paranthan, *Clayton 5263* (K, PDA). Anuradhapura District: Wilpattu National Park, East Intermediate Zone, along

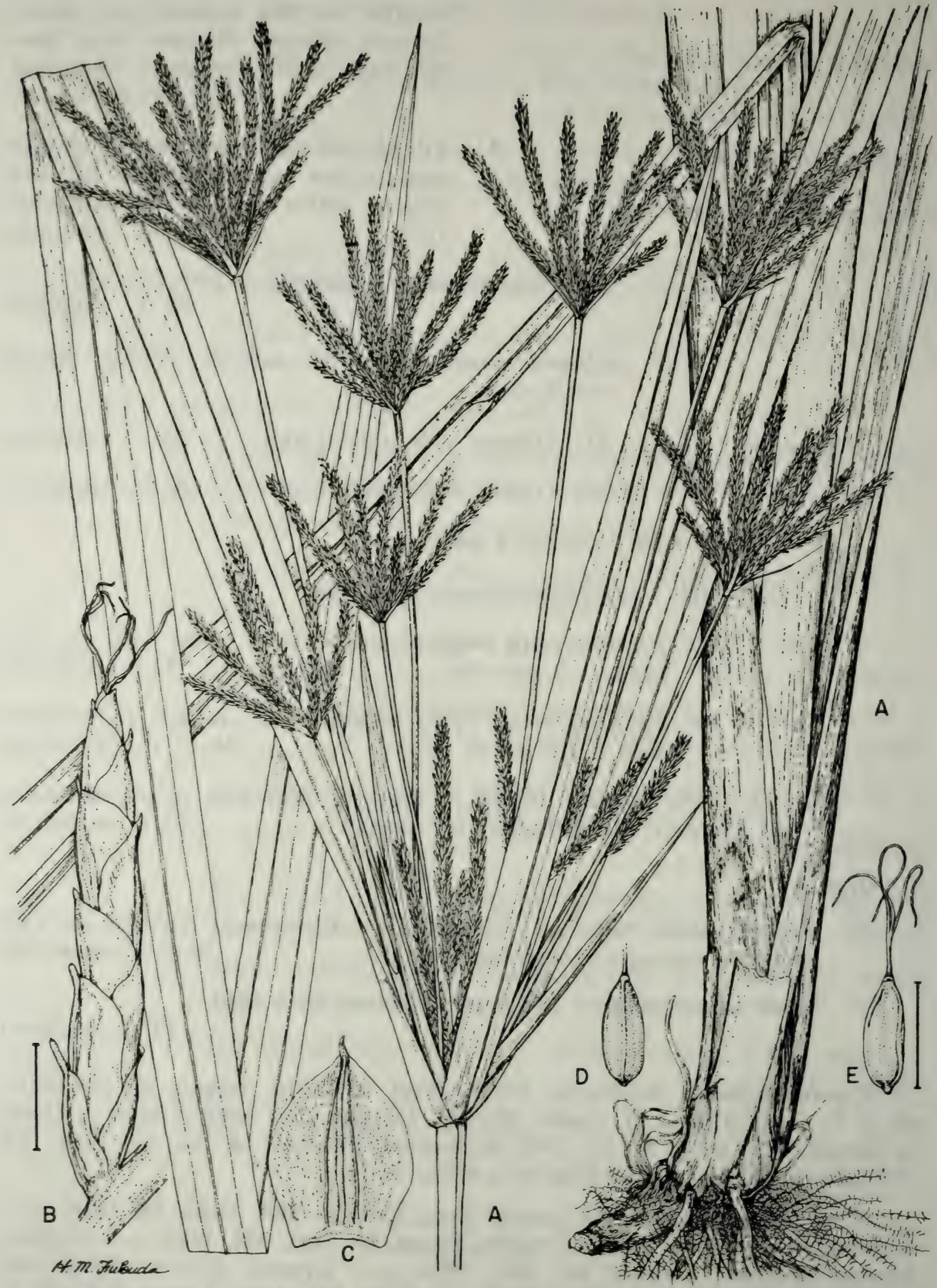

Fig.1. *Cyperus platyphyllus* Römer & Schultes. *AA*, habit. *B*, spikelet with its prophyll. *C*, glume. *D*, dorsal view of achene. *E*, ventral view of achene with style. Scales = 1 mm.

the Wildife Dept. trail, *ca.* 2 miles from barrier gate, *T. Koyama & Jayasuria 13965* (NY, PDA, US). Kandy District: Ramboda, *Thwaites C. P. 3043 ex p.* (K, PDA); Pusselawa, *Thwaites C. P. 3043 ex p.* (PDA). Colombo District: *Ferguson s.n.* (PDA).

Distribution. Pantropic with its range extending north into southern China and Formosa; abundant in South America and southern Asia, relatively scarce in tropical Africa and Australia.

Plants from India and Ceylon have often been treated as var. *hookeri*, which was segregated by its more copiously spiculose spikes. My observation of this species on a world-wide basis does not support this variety.

2. **Cyperus platyphyllus** Römer & Schultes, Syst. Veg. **2**: 876, 1817; C. B. Clarke, Fl. Brit. India **6**: 618, 1893, & Illustr. Cyper. *t. 20, f. 3-4*, 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 38, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1642, 1931; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 59, *f. 87*, 1935. — **Fig. 1.**

"*Cyperus elatus* L.," *sensu* Roxburgh, Fl. Indica ed. 1, **1**: 207, 1820. ——— *Cyperus roxburghii* Nees in Wight, Contrib. Bot. India 84, 1834; Thwaites, Enum. Pl. Zeyl. 70, 1864. ——— *Cyperus eminens* Klein ex Kunth, Enum. Pl. **2**: 70, 1837. ——— *Papyrus latifolia* Willdenow, Abhandl. Akad. Berlin 1812/13: 74, 1816.

Trincomalee District: Trincomalee, *Glenie* in 1864 (PDA). Matara District: Kukul Corale, *Thwaites C. P. 3041 ex p.* (K, PDA); Matara, *Trimen* 23 Feb. 1881 (PDA). Amparai District: Mile 205 on Rd. A 4,*ca.* 3 miles N of Pottuvilp, *T. Koyama et al. 14011* (NY, PDA, US).

Distribution. Confined to southern India and Ceylon. Marshy places at low altitudes.

This rather rare species is easily discernible by its sessile or nearly sessile spikes forming digitate secondary corymbs, and very broad leafy bracts and leaf blades. The distribution range of this species, covering the southern part of Indian Peninsula and Ceylon only, shows the same pattern as those of *Mariscus clarkei, Fimbristylis tenuifolia, Carex lobulirostris* and *Carex leucostachya.*

3. **Cyperus exaltatus** Retzius, Obs. Bot. **5**: 11, 1789; Thwaites, Enum. Pl. Zeyl. 343, 1864; C. B. Clarke, Fl. Brit. India **6**: 617, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 32, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 64, f. 9 A-F, 1935; Kern Reinwardtia **2**: 99, *f. 2*, 1952 & Fl. Males. I, **7** (3): 602, 1974.

Cyperus venustus R. Brown, Prodr. Fl. Nov. Holl. 217, 1810; Thwaites, Enum. Pl. Zeyl. 432, 1864. ——— *Cyperus altus* Nees in Wight, Contrib. Bot. India 84, 1834. ——— *Cyperus exaltatus* Retz. var. *amoenus* C. B. Clarke, Journ. Linn. Soc. **21**: 187, 1886; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 33, 1900.

Jaffna District: Jaffna, *Silva 110* (PDA); Murukan, *Silva* in 1917 (PDA). Vavunia District: Illukkulama, *ca.* 6 km SW of Vavunia, *T. Koyama & Herat 13603* (NY, PDA, US). Anuradhapura District: Anuradhapura, at margin of Nuwara Wewa Tank, *T. Koyama et al. 13939* (NY, PDA, US); Anuradhapura, *Brodin C. P.3040 ex p.* (PDA); Minneriya, *ca.* 15 miles E of Habarana, *T. Koyama et al. 13568* (NY, PDA, US). Mannar District: *ca.* 10 miles S E of Mannar, *T. Koyama et al. 13922* (NY, PDA, US). Polonnaruwa District: Yoda Ela, *Silva* in 1905 (PDA); Mannampitiya, *ca.* 5 miles ESE of Polonnaruwa, *T. Koyama & Herat 13572* (NY, PDA, US). Kandy District: Peradeniya, *Trimen C.P. 3040* in part (PDA). Badula District: *ca.* 8 miles E of Mahiyangana, 3.5 miles N. of Mile 53 on Mahiyangana-Padiyatalam Rd., *T. Koyama et al. 13980* (NY, PDA, US). Trincomalee District: Trincomalee, *Glenie C.P. 3788* (PDA). Batticaloa District: Batticaloa, *Trimen C.P. 3040* in part (PDA). Monaragala District: E of south end of Jayanthiwewa, *T. Koyama et al. 13988* (NY, PDA, US). Ratnapura District:

Fig. 2. *Cyperus pangorei* Rottboell. *AA*, habit. *B*, portion of spikelet showing two glumes and their bases forming wings on the rhachilla. *C*, spikelet. *D*, prophyll. *E*, glume. *F* & *G*, achenes. *H* & *J*, prophylls at the base of umbel ray. Scales = 1 mm.

Ratnapura, *Trimen C.P. 3040* in part (PDA); Ranwala, *Amaratunga 670* (PDA). Kurunegala District: Hettipola, *Amaratunga 670* (PDA); Uhuniya, *Amaratunga 182* (PDA). Ruhuna National Park: Andunoruwa Wewa, *Cooray* 16 Dec. 1969 (US).

Distribution. Pantropic, with its range extending northwards to eastern China and Japan. Rare in South America. In Ceylon very common in wet places at low altitudes, and often noted in rice fields.

4. **Cyperus papyrus** L., Sp. Pl. ed. 1, 47, 1753.

Kandy District: cultivated in the Botanic Gardens, Peradeniya, *Amaratunga* 197 (PDA). Native of East Tropical Africa with a subspecies in Madagascar. Widely cultivated in Ceylon as an ornamental.

5. **Cyperus corymbosus** Rottboell, Descr. Icon. Rar. Nov. Pl. 42, *t. 7 f. 4*, 1773; Thwaites, Enum. Pl. Zeyl. 344, 1864; C. B. Clarke, Fl. Brit. India **6**: 612, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 29, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1641, 1931; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 80, f. 10, 1936.

Anuradhapura District: between Ramboda and Madawachchiya, *T. Koyama & Herat 13602* (NY, PDA, US). Matale District: between Naula and Dambulla, vicinity of Mile 40, *Jayasuria 56* (US, PAD). Kandy District: Peradeniya, *Amaratunga 199* (PDA). Kegalle District: Baddewela, *T. Koyama & Samarakoon 13546* (NY, PDA, US). Badula District: 5 miles WNW of Mahiyangana, *Davidse 7595* (MO, NY, PDA). Batticaloa District: Vandeloos Bay, *T. Koyama & Herat 13579* (NY, PDA, US). Monaragala District: E of south end of Jayanthiwewa, *T. Koyama et al. 13987* (NY, PDA, US). Galle District: Moragoda, left bank of Bentota Ganga, *Amaratunga 2357* (PDA). Puttalam District: Irranonillu Madampe, *Amaratunga 2574* (PDA).

Distribution. Tropical West Africa, Madagascar, Nepal, India, Burma, northern Australia, West Indies and tropical South America (Venezuela and Brazil). Marshy places at low altitudes.

In Ceylon this species called *Gal-éhi* is occasionally more or less cultivated, because its straight culms are preferred by natives as material for making a kind of rough mats. The culms of *Scirpus grossus* L.f. are also used for the same purpose but is not cultivated.

6. **Cyperus articulatus** L., Sp. Pl. ed. 1, 44, 1753; Thwaites, Enum. Pl. Zeyl. 343, 1864; C. B. Clarke, Fl. Brit. India **6**: 611, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 29, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9:** 1641; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 77, 1936.

Polonnaruwa District: Kentalai, *Trimen* in 1885 (PDA). Batticaloa District: Batticaloa, *Thwaites C.P. 3561* (K, PDA).

Distribution. Mediterranean Region, Tropical Africa, India, Indo-China, southeastern U.S.A. to Central and South America. More frequent in the Neotropics.

It is rather interesting that this species has never been collected since Trimen's time.

7. **Cyperus pangorei** Rottboell, Descr. Icon. Rar. Nov. Pl. 31, *t. 7 f. 3*, 1773; Thawaites, Enum. Pl. Zeyl. 344, 1864; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 76, 1936. ——— **Fig. 2**.

Cyperus tegetum Roxburgh, Fl. Indica ed. 1, **1**: 208, 1820; C. B. Clarke, Fl. Brit. India **6**: 613, 1893, & Illustr. *t. 17, f. 1*, 1909. ——— *Cyperus dehiscens* (Nees) Nees, Linnaea **9**: 286, 1835; Kunth, Enum. Pl. **2**: 56, 1837; Trimen & Hook. f. Handb. Fl. Ceylon **5**: 30, 1900. ——— *Papyrus pangorei* (Rottb.) Nees in Wight, Contrib. Bot. India 88, 1834, in major part, concerning basionym. ——— *Papyrus dehiscens* Nees in Wight, l.c. 89, 1834.

Anuradhapura District: *ca.* 25 miles W of Trincomalee, along Rd. A 12, *T. Koyama et al. 14056* (NY, PDA, US); 2 km N of Yakalla, *T. Koyama 13595* (NY). Monaragala District: road between Maha Oya and Mullajama at Mile 14, *T. Koyama et al. 13981* (NY, PDA, US); Kotagoda, Siyambaladuwa to Inginiyagala, *Clayton 5825* (K, PDA). Colombo District: Ja-al on Gampaha Rd., *Comanor 1026* (US).

Distribution. Ceylon, India, Nepal and Burma. According to Kükenthal (op. cit.) also cultivated in Mauritius for mat-making.

Like *C. malaccensis* and *C. corymbosus* this species provides material for making mats. Trimen (op. cit.) mentions that in the Dambara area along Mahaweli Ganga this species is exclusively used for this purpose, and the mats are named after the locality.

8. **Cyperus bulbosus** Vahl, Enum. Pl. **2**: 342, 1806; C. B. Clarke, Fl. Brit. India **6**: 611, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 22, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1641, 1931; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 125, *f. 15 C-E*, 1936; Kern, Fl. Males. I, **7** (3): 605, 1974.

Puttalam District: Karapitiya, *Kundu & Balakrishnan 363* (US); Chilaw, *Ferguson,* Nov. 1881 (PDA). Trincomalee District: beach S of Elizabeth Point, sea level, *Davidse 7523* (MO, NY, PDA, US). Hambantota District: Ruhuna National Park, Patangala, beach, *Cooray* 16 Nov. 1969 (NY); Block III, 2 miles E. of Vaddangewardiya, N of Kataragama, *Wirawan 658* (NY).

Distribution. Tropical Africa, southern Asia, Malesia and northern Australia. Sandy beach; in Ceylon rather scarce.

In southern Asia the bulbs of this species is sometimes eaten by natives.

9. **Cyperus stoloniferus** Retzius, Obs. Bot. **4**: 10, 1786; C. B. Clarke, Fl. Brit. India **6**: 615, 1893 & Illustr. Cyper. *t. 19 f. 1-3,* 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 36, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 106, 1935; Blake, Univ. Queensl. Papers **2** (2): 9, *t. 7,* 1942; Kern, Fl. Males. I, **7** (3): 606, *f. 50,* 1974.

Jaffna District: Punkudutivu, lagoon edge, *Kundu & Balakrishnan 670* (US). Mannar District: End of the Causeway at Mile 145, *T. Koyama et al. 13923* (NY, PDA, US). Puttalam District: Puttalam Lagoon, ca. 6 miles N of Mampuri, *T. Koyama et al. 13912* (NY, PDA, US); Pallugaturai. W of Wilpattu National Park, *Davidse et al. 8217* (NY, PDA, US). Trincomalee District: Irrakkakandi, N of lagoon, *ca.* 12 miles NNW of Trincomalee, *T. Koyama et al. 14067* (NY, PDA, US). Colombo District: Negombo, *Simpson 7926* (PDA); Mount Lavinia, *Trimen* in 1981 (PDA); Kalagedihena, *Amaratunga 1406* (PDA).

Distribution. Madagascar, Mauritius, India, Indo-China, Malesia and Australia. In Ceylon rather frequent at margins of brackish lagoons, often forming a large community.

10. **Cyperus rotundus** L., Sp. Pl. ed. 1, 45, 1753; Thwaites, Enum. Pl. Zeyl. 343, 1864; C. B. Clarke, Fl. Brit. India **6**: 614, 1893; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 107, *f. 13,* 1935; S. T. Blake, Univ. Queensl. Papers **2** (2): 8, *t. 4,* 1942; Kern, Fl. Males. I, **7** (3): 604, *f. 49,* 1974.

Jaffna District: Jaffna, *Gardner C.P. 804,* ex p. (PDA). Anuradhapura District: Minneriya Tank, *Thwaites C.P. 804* ex p. (K, PDA); Anuradhapura, *Sinniah* in 1926 (PDA). Polonnaruwa District: Kanniyai, *Ramanathan 421* (PDA); Mile 79 on Rd. A 15, 1 m alt., *Davidse 7568* (MO, NY). Kurunegala District: Melsiripura, *Amaratunga 1333* (PDA). Matale District: Nalande, *Alston 640* (PDA). Kandy District: Peradeniya, *Thwaites C.P. 804* in part (PDA); Kadugannawa, *Alston 1089* (PDA); between Balana and Alagalla, *Comanor 1187*

(PDA, US); Haragama, *Alston* in 1926 (PDA); Gannoruwa, *Alston 300* (PDA); Katugastota, *Amaratunga 1088* (PDA).

Distribution. A cosmopolitan weed seen in tropical, subtropical and temperate regions of all the world.

11. **Cyperus tuberosus** Rottboell, Descr. Icon. Rar. Nov. Pl. 28, *t. 7 f. 1,* 1773; C. B. Clarke, Fl. Brit. India **6**: 616, 1893, in part.

Cyperus rotundus L. subsp. *tuberosus* (Rottb.) Kükenthal, Pflanzenr. **4** (20), 101 Heft: 113, 1936.

Trincomalee District: Trincomalee, *Ramanathan s.n.* (PDA). Polonnaruwa District: Polonnaruwa, *Alston 292* (PDA). Mannar District: opposite to Mannar, Mile 145 on A 14, end of the causeway, *T. Koyama et al. 13924* (NY, PDA, US); along Rd. A 14, Mile 123, near the junction with Madhu Rd., *T. Koyama et al.* 13918 (NY, PDA, US). Vavuniya District: Palayanalankulan, Mile 120 on Rd. A 14, *T. Koyama et al. 13936* (NY, PDA, US). Matale District: between Dambula and Habarane, at Mile 96 on Rd. A 6, *T. Koyama & Herat 13563* (NY, PDA, US); vicinity of Mile 40, between Naula and Dambula, *Jayasuria 59* (PDA).

Distribution. Eurasia.

12. **Cyperus retzii** Nees in Wight, Contrib. Bot. India 82, 1834.

Cyperus rotundus L. subsp. *retzii* (Nees) Kükenthal, Pflanzenr. **4** (20), 101 Heft: 114, 1935.

Central Province: without definite locality, *Thwaites C.P. 3750* (PDA).

Distribution. So far known from India, Ceylon and Australia; rare.

Thwaites' *C.P. 3750* cited above is the only Ceylonese collection of this species. In this specimen relatively broad spikelets ranging from 2.8 to 3.25 mm in width bear lance-ovate glumes which have two closely situated parallel veins on both sides of the mid-nerve and attain as much as 4 mm in length. Its achenes, average being 1.25 mm long, tend to be slightly larger than those of *C. rotundus.* Because of these characters the identity of *C.P. 3750* seems certain though I have not seen as yet the type of *C. retzii.*

13. **Cyperus scariosus** R. Brown, Prodr. 216, 1810; C. B. Clarke, Fl. Brit. India **6**: 612, 1893 & Illustr. Cyper. t. *15 f. 2-3,* 1909; S. T. Blake, Univ. Queensl. Papers **2** (2): 9, *t. 2,* 1942; Kern, Reinwardtia **2**: 103, f. 3, 1952 & Fl. Males. I, **7** (3): 607. 1974.

Cyperus corymbosus Rottb. var. *scariosus* (R. Br.) Kükenthal, Pflanzenr. **4** (20), 101 Heft: 83, 1935. ——— *Cyperus mitis* Steudel, Synops. Pl. Glumac. **2**: 316, 1855; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 103, 1935; Abeywickrama, Ceylon Journ. Sci., Biol. Sci., **2** (2): 134, 1959.

Jaffna District: between Poonaryn and Elephant Pass, along Jaffna Lagoon, *T. Koyama et al. 14048* (NY, PDA, US); Jaffna, *Silva* in 1920 (PDA); near Ampan, *Clayton 5235* (K, PDA); Keerimalai, Point Pedro, *Clayton 5203* (K, PDA); Puttalam District: between Puttalam and Kurunegala, *Trimen* Aug. 1883 (PDA); Madampe, *Amaratunga 2577* (PDA). Matale District: between Dambula and Habarane at Mile 96 on Rd. A 6, *T. Koyama & Herat 13564* (NY, PDA, US); Dambula, *Thwaites C.P. 3966* (K, PDA). Hambantota District: Tissamaharama, *Trimen* Dec. 1882 (PDA).

Distribution. Madagascar, India to Indo-China, Malesia, Australia.

Among very confusing nut-grasses *C. scariosus* can be easily recognizable by its filiform, obtuse-tipped spikelets which are only 1.5 to 2 mm wide. In Ceylon I saw this species growing together with *C. tuberosus* and *C. rotundus* respectively in two habitats, where I have seen no evidence of hybrids with the latter species.

Fig. 3. *Cyperus tenuiculmis* Steudel. *A*, habit. *B*, spikelet. *C*, prophyll at the base of spikelet. *D*, glume. *E*, lateral view of glume showing its hyaline extension of the base. *F*, achene.

Cyperus zollingeri steudel. *G*, cluster of spikelets. *H*, spikelet. *J*, portion of spikelet showing glumes and achenes. *K*, prophyll. *L*, glume. *M*, achene. = 1 mm.

14. **Cyperus sphacelatus** Rottboell, Descr. Pl. Rar. Progr. 21, 1772 & Descr. Icon. Rar. Nov. Pl. 26, 1773. Kükenthal, Pflanzenr. **4** (20), 101 Heft: 129, 1935; Kern, Reinwardtia **2**: 107, f. 5, 1952, & Fl. Males. I, **7** (3): 609, 1974.

Kandy District: Peradeniya, Univ. of Ceylon Campus, 500 m alt., *Comanor 321* (NY, US); ca. 5 miles SE of Gampaha, Mile 18/6 on Rd. A 5, 720 m alt., *Davidse et al. 7922* (MO, NY, PDA, US). Colombo District: Horana, *Alston 976* (PDA).

Distribution. Tropical America and tropical Africa; introduced to Ceylon, Malesia, Queensland and Tahiti.

The introduction of this species into Ceylon seems pretty old as it was already collected by Alston in the beginning of 1900.

15. **Cyperus tenuiculmis** Böckeler, Linnaea **36**: 286, 1870; Kern, Reinwardtia **3**: 30, 1954, & Fl. Males. I, **7** (3): 608, 1974. ——— **Fig. 3 A-F**

"*Cyperus zollingeri* Steudel" *sensu* C. B. Clarke, Fl. Brit. India **6**: 613, 1893, & Illustr. Cyper. t. 8 f. 1-2, 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 35, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 133, 1935.

Kandy District: Hantana, *Mueller-Dombois et al.* June 18, 1968 (PDA). Nuwara-Eliya District: Ramboda, 1180 m alt., *T. Koyama 13620* (NY); Hakgala, *Mueller-Dombois et al.* Jan. 1968 (PDA, US). Badulla District: *ca.* 8 miles E of Mahiyangana, 3.5 miles N of Mile 53 on Mahiyangana-Pediyatalawe Rd., *T. Koyama et al.* 13977 (NY, PDA, US); Diyatalawa, *Mueller-Dombois et al.* Jan. 14, 1968 (PDA). Monaragala District: E of the south end of Jayanthiwewa Tank, *T. Koyama et al. 13993* (NY, PDA, US).

Distribution. Throughout the tropics of the Old World with the range extending northwards to southern Japan in eastern Asia.

16. **Cyperus zollingeri** Steudel [in Zollinger, Syst. Verz **1**: 62, 1854, name only, &] Synops. Pl. Glumac. **2**: 17, 1855: Kern, Reinwardtia **3**: 28, 1954 & Fl. Males. I, **7** (3): 608, 1974. ——— **Fig. 3 G-M**

Cyperus ramosii Kükenthal in Fedde, Repert. Sp. Nov. 21: 326, 1925, & Pflanzenr. **4** (20), 101 Heft: 136, 1935; Kern, Reinwardtia **2**: 109, f. 7, 1952.

Hambantota District, Ruhuna National Park: Yala Dunes, Ecology Project Plot R26, *Cooray* 8 Dec. 1969 (NY, PDA, US); Block I, at Rugamtota, *Mueller-Dombois et al.* 7 Mar. 1969 (NY, US); Kumbukkan Oya, *ca.* 2 miles above mouth, at Magabakanda Meda Duwa, Block II, *Fosberg et al 51107* (NY, PDA, US).

Distribution. Tropical Africa, Madagascar, Malesia, northern Australia. In Ceylon rare in open grassy places on sandy soil.

New to the flora of Ceylon. This species differs from the better known *C. tenuiculmis* by the softer leaves and bracts, annual tufted habit without stolons, and smaller floral parts as illustrated in Fig. 3.

17. **Cyperus distans** L. f., Suppl. Sp. Pl. 103, 1781; Thwaites, Enum. Pl. Zeyl. 344, 1864; C. B. Clarke, Fl. Brit. India **6**: 607, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 30, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 137, 1935; Kern, Fl. Males. I, **7** (3): 610, 1974.

Polonnaruwa District: W of Siva Devale in Sacred Area Section 2A, *Ripley 369* (PDA). Kegalle District: Kadugannawa, *Grupe 213* (PDA, US). Nuwara Eliya District: Hakgala Botanic Garden, *Clayton 5784* (K, PDA); Maturata, *Ferguson* in 1906 (PDA). Kandy District: Peradeniya, *Thwaites C.P. 810* ex p. (K, PDA); Gannoruwa, *Alston 319* (PDA); *ca.* 2 miles E. of Maddakele, slope N.W. of Kunckles Peak, 1440 m alt., Davidse 8320 (MO, NY, PDA, US). Batticaloa District: Batticaloa, *Thwaites C.P. 810* in part (PDA).

Distribution. Pantropic.

18. **Cyperus nutans** Vahl, Enum. Pl. **2**: 363, 1806; C. B Clarke, Fl. Brit. India **6**: 607, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 31, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1640; 1931; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 144, *f. 5 A-D*, 1935; Kern, Fl. Males. I, **7** (3): 609, 1974.

Cyperus distans L. var. *major* Thwaites, Enum. Pl. Zeyl. 432, 1864.

18a. Subsp. **nutans.**

Anuradhapura District: Anuradhapura, *Thwaites* in 1881 (PDA); Wilpattu National Park, *ca.* 2.7 miles to Ranger's Office along pass from southern entrance, *T. Koyama & Jayasuria 13967* (NY, PDA, US). Trincomalee District: Trincomalee, *Brodie C.P. 3844* (PDA). Matale District: Dambulla, *Thwaites C.P. 3966* in part (PDA). Colombo District: Galapitamada, *Amaratunga 1148* (PDA). Monaragala District: E of south end of Jayanthiwewa Tank, *T. Koyama et al. 13992* (NY, PDA, US). Hambantota District: Ruhuna National Park, Yala Plain, *Comanor 863A* (NY, US).

Distribution. India. southern China and Malesia.

18b. Subsp. **eleusinoides** (Kunth) T. Koyama, *stat. nov.*

Cyperus eleusinoides Kunth, Enum. Pl. **2**: 29, 1937; C. B. Clarke, Fl. Brit. India **6**: 608, 1893; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 144, 1936. ——— *Cyperus nutans* Vahl var. *eleusinoides* (Kunth) Haines, Bot. Bihar Orissa **5**: 898, 1924; Kern, Fl. Malesiana I, **7** (3): 610, 1974.

Kandy District: Haragama, *Trimen C.P. 3044* (PDA). Hambantota District: Ruhuna National Park, *Mueller-Dombois et al.* Jul. 1967 (PDA).

Distribution. Tropical Africa, India to Malesia and northern Australia, also extending northwards to the Ryukyus.

Cyperus nutans and *C. eleusinoides* are very similar to one another, and the only reliable difference between the two is the more densely disposed, longer spikelets in the latter. But, this difference becomes obscure as ssp. *subprolixus* of the Ryukyus and Taiwan comes between the two as to the density and the number of florets in the spikelet. I, therefore, regard *C. eleusinoides* as a subspecies of *C. nutans.*

19. **Cyperus procerus** Rottboell, Descr. Icon. Rar. Nov. Pl. 29, *t. 5 f. 3*, 1773; Thwaites, Enum. Pl. Zeyl. 343, 1864; C. B. Clarke, Fl. Brit. India **6**: 610, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 34, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 91, 1935; Kern, Fl. Males. I, **7** (3): 611, f. 51, 1974. ——— **Fig. 4**

Jaffna District: Murunkan, *Silva* in 1917 (PDA). Vavunia District: Vavunia, *Clayton 5306* (K, PDA); near Kokkavil, *Clayton 5292* (K, PDA). Anuradhapura District: Anuradhapura, *Trimen* Dec. 1884 (PDA); Alankulam, *Trimen* Oct. 1883 (PDA); Mile 123 on Rd. A 14, E of Medachchiya, *T. Koyama et al. 13921* (NY, PDA, US). Wilpattu National Park: Kuda Pathessa, *T. Koyama & Herat 13394* (NY, PDA, US); Periya Naga Villu, *Wirawan et al. 903* (US); Manikepola Uttu, *T. Koyama 13461* (NY, PDA, US); Wilpattu West Sanctuary, Mari Villu, *T. Koyama 13972* (NY, PDA, US). Batticaloa District: Batticaloa, *Thwaites C.P. 3752* (K, PDA); Ottawady, opposite to Valaichchenai, *T. Koyama & Herat 13582* (NY, PDA, US). Mannar District: Murunkan, *Silva* in 1917 (PDA); Illupadichchanai, *Lord s.n.* (PDA). Puttalam District: Madampe, *Amaratunga 2575* (PDA). Matale District: Dambulla, *Thwaites C.P. 3752* in part (K, PDA); between Naula and Dambula, vicinity of Mile 40, *Jayasuria 60* (PDA). Kandy District: Siyambalatenna, *Alston 390* (PDA); Peradeniya, *Thwaites C.P. 802* (PDA), *Alston 1181* (PDA). Kurunegala District: Kurunegala. *Thwaites C.P. 3752* in part (PDA). Colombo District: Colombo, *Ferguson s.n.* (PDA). Hambantota District: Tissamaharama, *Alston 1179* (PDA); Ruhuna National Park, Block II, 7 m alt.,

Fig. 4. *Cyperus procerus* Rottboell. *AA*, habit. *B*, spikelet. *C*, prophyll. *D*, glume. *E*, achene. Scales for floral parts = 1 mm.

Comanor 1037 (PDA), US). Amparai District: Helawe Eliya, *ca.* 7 miles S. of Panama, E. of Helawe Lagoon, *T. Koyama et al. 14024* (NY, PDA, US).

Distribution. India, Ceylon, Indo-China, Taiwan, Malesia, Australia (Queensland). In Ceylon abundant in marshy places at low altitude.

20. **Cyperus pilosus** Vahl, Enum. Pl. **2**: 354, 1806; Thwaites, Enum. Pl. Zeyl. 344, 1864; C. B. Clarke, Fl. Brit. India **6**: 609, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 32, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 92, 1935; Kern, Fl. Malesi I, **7** (3): 611, *f. 52,* 1974.

Cyperus marginellus Nees in Wight, Contrib. Bot. India 83, 1834. —— *Cyperus obliquus* Nees in Wight, l.c. 86, 1834.

Nuwara Eliya District: between Pussellawa and Ramboda, Mile 32/8 on Nuwara-Eliya-Kandy Rd., 1000 m alt., *T. Koyama 13617* (NY, PDA, US). Badulla District: Haptale, *Silva* in 1906 (PDA). Kandy District: Rangala, *Ferguson* Sept. 1885 (PDA). Kalutara District: Korosduwa, *Amaratunga 2541* (PDA); Kande Kanda, *Amaratunga 2523* (PDA). Kegalle, District: Kegalle, *Amaratunga 1651* (PDA); Kattiyakumbura, *Amaratunga 1589* (PDA); Nayinankada, 700 m alt., *T. Koyama & Samarakoon 13561* (NY, PDA, US). Kurunegala District: Naramunala, *Amaratunga* in 1966 (PDA); Malsiripura, *Amaratunga 1330* (PDA). Ratnapura District: 11 miles E of Deniyaya at Mile 62 on Rd. A 17, 750 m alt., *Davidse 7876* (MO, NY, PDA, US). Galle District: Akeemana, *Alston 1187* (PDA); Moragoda, *Amaratunga 2359* (PDA). Monaragala District: Inginiyagala National Park, between Baduluwila and "Westminster Abbey", *T. Koyama et al. 13994* (NY, PDA, US); E of south end of Jayanthiwewa, *T. Koyama et al. 13988* (NY, PDA, US).

Distribution. Rather widely distributed in tropical and subtropical regions of the Old World from tropical West Africa through Central Asia and Indian Sub-Continent eastwards to Malesia and northern Australia. In eastern Asia the range extending northwards as far as to warm-temperate Japan.

Although this species is highly variable in the dimension of leaves and inflorescences, it is well demarcated by the subdensely hispid rhachis of spikes.

21. **Cyperus compressus** L., Sp. Pl. ed. 1, 46, 1753; Thwaites, Enum. Pl. Zeyl. 342, 1864; C. B. Clarke, Fl. Brit. India **6**: 605, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 33, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 156, *f. 4 A-D,* 1935; Kern, Fl. Males. I, **7** (3): 617,1974.

21a. Subsp. **compressus.**

Jaffna District: Jaffna, *Trimen* Feb. 1890 (PDA), *Silva* in 1920 (PDA). Vavunia District: S of Mullaittivu, *Fosberg & Balakrishnan 53527* (NY, US). Polonnaruwa District: Gal Oya Reservoir, near the spilway, 270 m alt., *Comanor 561b* (US). Trincomalee District: 7 miles S of Dambulla on Kandy Rd., *Clayton 5078* (K, PDA); between Naula and Dambulla, vicinity of Mile 40, *Jayasuria 57* (PDA). Kurunegala District: Kurunegala, *Thwaites C.P. 812* (K, PDA). Kandy District: Peradeniya, *Trimen C.P. 812* (PDA); Kandy, *Alston* in 1926 (PDA). Colombo District: Danowita, *Amaratunga 1450* (PDA). Hambantota District: Ruhuna National Park, Gonalabbe, Block I, *Cooray & Balakrishnan* 20 Jan. 1969 (US). Monaragala District: E of the south end of Jayanthiwewa, *T. Koyama et al. 13991* (NY, PDA, US); way to Nilgola, *Trimen* Jan. 1888 (PDA); Inginiyagala, *Amaratunga 1706* (PDA).

Distribution. Cosmopolitan; tropical, subtropical and temperate regions of all world; weed of cultivated and waste places, more frequent along sea coast.

21b. Subsp. **micranthus** T. Koyama, *subsp. nov.*

Planta omnibus partibus minor; inflorescentia semper in capitulum unicum congesta; glumae 2 mm longae; achaenia obovato-orbicularia, basi valde attenuantia, vix 1 mm longa, 0.75 mm lata; caeteroquin sicut ssp. *compressus.*

Trincomalee District: exposed eastern bottom of Kantalai Tank at Mile 134 on Habarana-Trincomalee Rd., *Davidse 7561* (NY, holotype; MO, isotype).

Distribution. Thus far known only by the collection cited above.

Subspecies *micranthus* differs from the typical phase primarily by the smaller glumes (2 mm vs. *ca.* 3.5 mm in length) and achenes (1 by 0.75 mm vs. 1.5 by 1 mm in size) in addition to its comparatively smaller habit with always congested inflorescences. Besides the fertile achenes every detail of floral parts shows no evidence of the possible hybrid nature of this subspecies, though it has been known that *C. compressus* rather freely hybridize with several species. So far I have not come across as yet any specimen of *C. compressus* bearing such smaller glumes and achenes from its total range.

22. **Cyperus iria** L., Sp. Pl. ed. 1, 45, 1753; Thwaites, Enum. Pl. Zeyl. 344, 1864; C. B. Clarke, Fl. Brit. India **6**: 606, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 18, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 150, 1935; Kern, Fl. Males. I, **7** (3): 616, 1974.

Jaffna District: *Jaffna,* Silva Nov. 1920 (PDA). Trincomalee District: Trincomalee, *Ramanathan* Jul. 1926 (PDA). Anuradhapura District: Mile 123 on Rd. A 14, *T. Koyama et al. 13920* (NY, PDA, US); Wilpattu National Park, Manikepola Uttu, *T. Koyama & Jayasuria 13951* (NY, PDA, US). Matale District: between Mirisgoniyawa and Dambulla, *Silva* Nov. 1926 (PDA); between Naula and Dambulla, vicinity of Mile 40, *Jayasuria 55* (PDA); Matale North, *Jayasuria 53* (PDA). Kandy District: Peradeniya, *Trimen C.P. 811* (K, PDA); Pundaluoya, *Hughes* Dec. 1902 (PDA). Kurunegala District: Kurunegala, *Thwaites C.P. 811* in part (PDA). Colombo District: Giriulla, *Amaratunga 998* (PDA); Veyangoga, *Amaratunga 1946* (PDA). Kalutara District: Bolgoda, *Amaratunga 2524* (PDA). Ruhuna National Park: Buttawa Plain, near Ecology Project Plot R35, *Cooray* 12 Dec. 1969 (US); Yala Plain, Patanagala Beach, 3 m alt., *Comanor 863B* (NY, US).

Distribution. Widely distributed in Asia from Iran and Afghanistan through Indian Subcontinent northeastwards to China and Japan, and eastwards to Malesia and Australia; also in East Africa. Apparently introduced to southeastern U.S.A., West Indies and South America. Common weed in cultivated ground and rice field.

23. **Cyperus diffusus** Vahl, Enum. Pl. **2**: 321, 1806; C. B. Clarke, Fl. Brit. India **6**: 603, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 28, 1900 Kükenthal, Pflanzenr. **4** (20), 101 Heft: 208, 1936; Kern, Fl. Males. I, **7** (3): 619, 1974.

Cyperus nigro-viridis Thwaites, Enum. Pl. Zeyl. 344, 1864.

23a. Subsp. **diffusus.**

Kurunegala District: Kurunegala, *Thwaites C.P. 2879* (PDA).

Distribution. India, Indo-China, southern China and Malesia.

23b. Subsp. **macrostachyus** (Böckleler) T. Koyama, *stat. nov.*

Cyperus diffusus Vahl var. *macrostachyus* Böckeler, Linnaea **35**: 534, 1868; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 28, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 209, 1936; Kern, Fl. Males. I, **7** (3): 619, f. 54, 1974. ——— *Cyperus pubisquama* Steudel [in Zollinger, Syst. Verz. **1**: 62, 1854, nomen,] Synops. Pl. Glumac. **2**: 20, 1855.

Kurunegala District: Kurunegala, *Thwaites C.P. 3931* (PDA); Mallawapitiya, *Amaratunga 1101* (PDA); Athagala, *Amaratunga 678* (PDA). Matale District: Matale, *Ferguson* Oct. 1884 (PDA).

Distribution. From India through Indo-China eastwards to Malesia.

Subspecies *macrostachyus* differs from the typical phase in its generally larger habit, far more copious inflorescence and longer spikelets as mentioned in the key to species. In Ceylon subsp. *diffusus* is very rare, and has so far been documented only by *Thawaites C.P. 2879.*

24. **Cyperus platystylis** R. Brown, Prodr. Fl. Nov. Holl. 214, 1810; C. B. Clarke, Fl. Brit. India **6**: 598, 1893; Trimen & Hook, f., Handb. Fl. Ceylon **5**: 24, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1639, 1931; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 185, *f. 21,* 1936; Kern, Fl. Males. I, **7** (3): 618, 1974. ——— **Fig. 5**

Cyperus pallidus Nees [Linnaea **9**: 284, 1835, nomen nudum, &] in Wight, Contrib. Bot. India 79, 1834; Thwaites, Enum. Pl. Zeyl. 34, 1864. Not of Willdenow ex Link, 1820, nor of Savi, 1830. ——— *Anosporum pallidum* (Nees) Böckeler, Linnaea **36**: 412, 1870.

Kurunegala District: Kurunegala, *Trimen C.P. 3559* in part (PDA); Wariyapola, *Amaratunga 1104* (PDA). Batticaloa District: Kalmunai, *Ahmed* Aug. 1940 (PDA); Batticaloa *Trimen C.P. 3559* in part (K, PDA). Amparai District: Lahugala Tank, *T. Koyama et al. 14030* (NY, PDA, US). Colombo District: Muturajawela, *Amaratunga 144* (PDA).

Distribution. India and Ceylon to Taiwan, and through Malesia eastwards to northern and eastern Australia. In marshes and ponds usually growing in large communities.

This rare species is easily discernible in its achenes with spongy thickened angles and densely spiculose hemisphaerical umbel. The rhizomes are often more or less elongated and obliquely ascending, but do not emit stolons.

25. **Cyperus alternifolius** L., Mant. **2**: 28, 1771.

This species, known from East Africa and Madagascar, is represented in Ceylon by the following.

Subsp. **flabelliformis** (Rottboell) Kükenthal, Pflanzenr. **4** (20), 101 Heft: 193, 1936.

Cyperus flabelliformis Rottboell, Descr. Pl. Rar. Progr. 22, 1772, & Descr. Icon. Rar. Nov. Pl.. 42, *t. 12 f. 2,* 1773.

Badulla District: Rawanaella Waterfall, *ca.* 2 miles SE of Ella, Mile 13, 780 m alt., *Davidse et al. 8858* (MO, NY, PDA, US). Monaragala District: 4 miles N of Wellawaya, *Wheeler 12689* (PDA, US).

Distribution. A native of tropical Africa and Arabia. Widely cultivated as an ornamental; in Ceylon escaped and established in grassy places.

26. **Cyperus radians** Nees & Meyen [ex Nees, Linnaea **9**: 285, 1835, nomen nudum,] ex Kunth, Enum. Pl. **2**: 95, 1837, as *"radicans";* C. B. Clarke, Fl. Brit. India 6: 605, 1893; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 214, 1936; Kern, Fl. Males. I, **7** (30): 623, 1974.

Trincomalee District: seashore several miles E of Toppur, *ca.* 15 miles SE of Trincomalee, *T. Koyama 14060b.* (NY).

Distribution. Indo-China, Malay Peninsula, southeastern China, Borneo. Sporadically noted in sandy sea coast.

New to the flora of Ceylon. The above collection marks a considerable range extension of this southeastern Asian species into the Indian Subcontinent. This is a

Fig. 5. *Cyperus platystylis* R. Brown. *AA*, habit. *B*, spikelet. *C*, glume. *D*, dorsal view of achene. *E*, ventral side of achene. Scales = 1 mm.

peculiar looking species growing in sand. Since the culms are normally extremely abbreviated and hidden in the leaf tuft, the elongated umbel rays look like tufted culms.

27. **Cyperus pulcherrimus** Willdenow ex Kunth, Enum. Pl. **2**: 1837; C. B. Clarke, Fl. Brit. India **6**: 600, 1893, & Illustr. Cyper. *t. 10 f. 1-3,* 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 27, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 242, 1936; Kern, Fl. Males. I, **7** (3): 624, 1974.

"*Cyperus silletensis* Nees" *sensu* Thwaites, Enum. Pl. Zeyl. 343, 1864.

Wilpattu National Park: between Kattankandal Kulam and Occapu Junction, *Wirawan et al. 977* (US); Manikepola Uttu, *T. Koyama et al. 13462* (NY, PDA, US); between Kunbuk Wila and Kokkare Villu, *T. Koyama & Jayasuria 13946b* (NY); Malimaduwa Guards Quater, *Wirawan & Cooray 1141* (NY, PDA). Batticaloa District: Batticaloa, *Trimen C.P. 3558* (K, PDA). Kurunegala District: Kurunegala, *Rasanayaka* in 1927 (PDA). Matale District: 8 miles E. of Habarane, *T. Koyama & Herat 13567* (NY, PDA, US). Colombo District: Kotugoda, *Amaratunga 2027 & 2262* (PDA).

Distribution. India, Indo-China, Malesia.

28. **Cyperus haspan** L., Sp. Pl. ed. 1, 45, 1753; Thwaites, Enum. Pl. Zeyl. 343, 1864; C. B. Clarke, Fl. Brit. India **6**: 600, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 26, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 247, *f. 28 E-G,* 1936; Kern, Fl. Males. I, **7** (3): 624, *ff. 56 & 57,* 1974.

Anuradhapura District: Anuradhapura, *Brodie C.P. 799* (K, PDA); Wilpattu National Park, Manikepola Uttu, *T. Koyama & Jayasuria 13953* (NY, PDA, US). Trincomalee District: Trincomalee, *Glenie C.P. 799* in part (PDA); Periya Kulam, *ca.* 7 miles NW of Trincomalee, *T. Koyama et al. 14066* (NY, PDA, US). Puttalam District: Wilpattu West Sanctuary, Marai Villu, *T. Koyama 13973* (NY, PDA, US); Madape, *Amaratunga 2569* (PDA). Vavunia District: Kokkavil, *Clayton 5294* (K, PDA). Nuwara Eliya District: Rangalla to Corbett's Gap, *Ballard 1416* (K, NY). Kurunegala District: Kurunegala, *Rasanayake* in 1927 (PDA); Ibbagamuwa, *Amaratunga 1581* (PDA). Kandy District: Peradeniya, *Alston 311* (PDA); Upper Hantana Rd., *Comanor 314* (PDA, US); Hantane, *Thwaites C.P. 965* in part (K, PDA). Kegalle District: Alapalawala, along river Watura Oya, *ca.* 500 m alt., *T. Koyama & Samarakoon 13558* (NY, PDA, US); Mawanella, *Amaratunga 1199* (PDA). Badulla District: Rd. A 4, *ca.* 3 miles W of Koslanda, *ca.* 900 m alt., *T. Koyama et al. 14032* (NY, PDA, US). Ratnapura District: 11 miles E of Deniyana at Mile 62 on Rd. A 17, 750 m alt., *Davidse 7885* (MO, NY, PDA, US); Kuruwita, *Trimen* in 1895 (PDA). Colombo District: Muthurajawela, *Amaratunga 135* (PDA). Kalutara District: Nugegoda, Bolgoda Lake Scheme, *Amaratunga 2538* (PDA). Galle District: Galle, *Thwaites C.P. 965* (PDA): Bentota Ganga, *Amaratunga 2332* (PDA); Ambalangoda, *Amaratunga 2642* (PDA). Monaragala District: *ca.* 3 miles W. of Wellawaya at Mile 135/10 on Rd. A 4, 990 ft. alt., *Davidse 7731* (MO, NY).

Distribution. Tropical and subtropical regions of all the world with its range extending northwards into Japan in East Asia. Abundant in wet places; frequent in rice fields.

This species is sometimes divided into two subspecies, ssp. *haspan* and ssp. *junciformis* Kükenthal, the latter differing from the typical phase in having long-creeping rhizome along which the culms are disposed in a row in a more or less spaced manner. In plants from Asia these two subspecies seem quite well circumscribed, and consequently, appear to be recognizable. Typical ssp. *haspan,* with the culms tufted without conspicuous rhizome, is often confused with closely related *C. tenuispica.* The only reliable character to separate these two are floral glumes. In *C. tenuispica* the floral glumes are spaced exposing a considerable part of the subtending achene between two glumes, while in *C. haspan* the achenes are completely hidden by the closely disposed glumes.

29. **Cyperus tenuispica** Steudel, Synops. Pl. Glumac. **2**: 11, 1855; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 245, *f. 28 A-D,* 1936; Kern, Fl. Males. I, **7** (3): 625, *f. 58,* 1974.

"*Cyperus flavidus* Retzius" sensu C. B. Clarke, Fl. Brit. India 6: 600, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 27, 1900.

Jaffna District: Mullaitiva, *Ferguson s.n.* (PDA); south shore of Jaffna Lagoon, *ca.* 8 miles SE of Poonaryn, *T. Koyama et al. 14046* (NY, PDA, US). Wilpattu National Park; Kuda Pathessa, *T. Koyama 13387* (NY). Matale District: Matale north, *Jayasuria 54* (PDA). Kandy District: Paradeniya, *Alston* in 1926 (PDA), *Trimen C.P. 805* (PDA); Gannoruwa, *Alston 315* (PDA). Colombo District: Gampaha, *Simpson 8602* (PDA); Makawita, *Amaratunga 1779* (PDA). Hambantota District: Ruhuna National Park, Block I, Rakinawala, *Cooray* 7 Dec. 1969 (US).

Distribution. Tropical Africa, India, Nepal, Indo-China, Malesia, southeastern China, Japan. Wet places; often as a weed in rice field.

30. **Cyperus difformis** L., Cent. Pl. **2**: 6, 1756; C. B. Clarke, Fl. Brit. India **6**: 599, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 25, 1900; Kükenthal Pflanzenr. **4** (20), 101 Heft: 237, f. 27 F-H, 1936; Kern, Fl. Males. I, **7** (3): 629, 1974.

Trincomalee District: Trincomalee, Ramanathan in 1926 (PDA). Polonaruwa District: *ca.* 1 mile E of Kolakanaweli, at Mile 56/7 on Rd. A 11, *T. Koyama 13577* (NY). Batticaloa District: Batticaloa, *Thwaites C.P. 3042* (K, PDA). Kandy District: Gannoruwa, *Alston 316* (PDA). Matale District: Ereula Tank, *ca.* 5 miles SE of Dambulla, 650 ft. alt., *Davidse 7390* (MO, NY). Colombo District: Danowita, *Amaratunga 192* (PDA). Amparai District: Tandiadi Kalapu Lagoon, S of Mile 215 on Rd. A 4, *T. Koyama et al. 14015* (NY, PDA, US). Ruhuna National Park: Komawa Wewa, Cooray 10 Dec. 1969 (NY), US); Uraniya, Cooray 22 Mar. 1970 (NY).

Distribution. Widely distributed in Eurasia from southern Europe through India and China to Japan and Malesia, also in Pacific Islands and Australia; introduced to Central America and South Africa possibly with rice.

31. **Cyperus castaneus** Willdenow, Sp. Pl. **1**: 278, 1797; Thwaites, Enum. Pl. Zeyl. 343, 1864; C. B. Clarke, Fl. Brit. India **6**: 598, 1893; Trimen & Hooks. f., Handb. Fl. Ceylon **5**: 25, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 264, 1936; Kern, Fl. Males. I, **7** (3): 630, 1974.

Anuradhapura District: Wilpattu National Park, East Intermediate Zone, along Wildlife Dept. Path, *ca.* 2 km from its barrier gate, *T. Koyama & Jayasuria 13966* (NY, PDA, US). Polonnaruwa District: SE of Giritale Wewa near Circuit Bangalow, *Fosberg et al. 51955* (PDA, US); Polonnaruwa, *Clayton 5115* (K, PDA). Matale District: Dambulla Rock, *Trimen* in 1896 (PDA). Kegalle District: *Simpson 8358* (PDA). Badulla District: between Ratupahana and Haldunmulla, *Ormiston* in 1909 (PDA). Ruhuna National Park: Block I, *Cooray* 7 Dec. 1969 (US); between Buttawa and Karangaswela, *Cooray* 3 Dec. 1969 (NY, US).

Distribution. From India through Indo-China to Malesia and northern Australia.

32. **Cyperus cuspidatus** Kunth in Humb., Bonpl. & Kunth, Nov. Gen. et Sp. Pl. **1**: 204, 1815; C. B. Clarke, Fl. Brit. India **6**: 598, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 26, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 261, *f. 29 E,* 1936; Kern, Fl. Males. I, **7** (3): 629, *f. 59,* 1974.

Cyperus angustifolius Nees in Wight, Contrib. Bot. India 79, 1834.

Anuradhapura District: Wilpattu National Park NE of Kuruttu Pondi Villu, *T. Koyama 13413* (NY). Polonnaruwa District: 7 miles NW of Polonnaruwa, SE of Giritale Wewa, *Fosberg & Ripley 51955* (US). Nuwara Eliya District: *ca.* 15 miles NW of Nuwara Eliya, at Mile 32/8 on Road A 5, 1020 m alt., *Davidse et al. 7946* (MO, NY, PDA). Monaragala District: Inginiyagala National Park, between Baduluwila and "Westminster Abbey," *T. Koyama et al. 13997* (NY, PDA, US); *ca.* 25 miles W of Pottuvil on road to Wellawaya, near Mile 76, *Davidse et al. 8934* (MO, NY, PDA). Hambantota District: Ruhuna National Park, Karasugaswela, *Cooray* 12 Dec. 1969 (NY, PDA).

Distribution. Pantropic, with its range extending north to southern China and Formosa.

33. **Cyperus arenarius** Retzius, Obs. Bot. **4**: 9, 1786; Nees in Wight, Contrib. Bot. India 77, 1834; Thwaites, Enum. Pl. Zeyl. 342, 1864; C. B. Clarke, Fl. Brit. India **6**: 602, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 23, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1640, 1931; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 270, 1936. ——— **Fig. 6**

Bobartia indica L., Fl. Zeyl. 17, 1747. ——— *Cyperus conglomeratus* Rottb. var. *arenarius* (Retzius) Cosson, Explor. Algir. Bot. **2**: 245, 1855.

Mannar District: Talaimannar, *Silva* in 1916 (PDA). Trincomalee District: Trincomalee, *Glenie C.P. 798* (K, PDA); Puttalam District: Kalpitiya, *Trimen* in 1883 (PDA); Chilaw, Trimen in 1880 (PDA); Wilpattu National Park, West Intermediate Zone, Pallugaturai Beach, *Wheeler 12104* (PDA). Batticaloa District: Passikudah, *Mueller-Dombois* in 1968 (PDA); Batticaloa, *Gardener C.P. 798* (PDA). Colombo District: Colombo, *Ferguson C.P. 794* (PDA); Uswetakeiyawa, *Amaratunga 126* (PDA). Amparai District: Pottuvil, Rest House beach, *Balakrishnan 389* (PDA); Arugam Bay, *T. Koyama et al. 14029* (NY, PDA, US), *Fosberg & Sachet 53043* (NY, US). Hambantota District: Bentota, beach behind rest house, *Ballard 1510* (K, PDA); Ruhuna National Park, beach E of Buttawa Modera, 2-3 m alt., *Fosberg 50315* (US); Patanagala Beach, *Cooray* 17 Nov. 1969 (PDA, US).

Distribution. Southern Iran, Pakistan, India, Ceylon, Cochinchina.

A coastal species easily reconginable by the whitish head with broad spikelets and extensive rhizome system, with which it usually forms a large pure community.

34. **Cyperus conglomeratus** Rottboell, Descr. Icon. Rar. Nov. Pl. 21, *t. 15 f.7*, 1773; Thwaites, Enum. Pl. Zeyl. 343, 1864; C. B. Clarke, Fl. Brit. India **6**: 602, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 23, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 272, *f. 30*, 1936.

Cyperus pachyrrhizus Nees ex Böckeler, Linnaea **35**: 545, 1868; C. B. Clarke, Fl. Brit. India **6**: 603, 1893; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1640, 1931. ——— *Cyperus conglomeratus* Rottb. var. *pachy*[*r*]*rhizus* (Nees ex Böckeler) Trimen in Trimen & Hook. f, Handb. Fl. Ceylon **5**: 23, 1900.

Puttalam District, Wilpattu National Park: Kollankanatta Beach, *Cooray* 28 Sept. 1969 (US); Pallugaturai, *T. Koyama & Jayasuria 13960* (NY, PDA, US), *Fosberg et al. 50917* (NY, US), *Wheeler 12105* (PDA).

Distribution. Mediterranean Region, North Africa, East Africa, Iran, Arabia, Madagascar, southern India and Ceylon.

This is one of the western Asian element reaching Ceylon. Having compared a good series of Indian and Ceylonese specimens with those from western Asia I am unable to separate Indian plants from western Asian ones.

35. **Cyperus cephalotes** Vahl, Enum. Pl. **2**: 311, 1806; C. B. Clarke, Fl. Brit. India **6**: 597, 1893, & Illustr. Cyper. *t. 6 f. 1-7*, 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 17, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 292, 1936; Kern, Fl. Males. I, **7**(3): 633, *ff. 61-62*, 1974.

Fig. 6. *Cyperus arenarius* Retzius. *A*, habit. *B*, spikelet. *C*, prophyll. *D*, glume. *E*, pistil. *F*, achene. Scales = 1 mm.

Cyperus hookerianus Thwaites, Enum. Pl. Zeyl. 342, 1864. ——— *Anosporum cephalotes* (Vahl) Kurz, Journ. Asiat. Soc. Bengal **45** (2): 159, 1876.

Kurunegala District: Ibbagamuwa, *Amaratunga* in 1967 (PDA).

Distribution. From India through Indo-China northeastwards to southern China, and eastwards to Malesia and northern Australia.

Trimen (op. cit.) reported this species from Galle, Lunugala and Uva. Currently in the Peradeniya Herbarium the specimen cited above is the only sheet.

36. **Cyperus alopecuroides** Rottboell, Descr. Pl. Rar. Progr. 20, 1772, & Descr. Icon. Rar. Nov. Pl. 38, *t. 8 f. 2,* 1773; Thwaites, Enum. Pl. Zeyl. 342, 1864; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 38, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 71, 1935; Kern, Fl. Males. I, **7** (3): 603, 1974

Juncellus alopecuroides (Rottb.) C. B. Clarke, Fl. Brit. India **6**: 595, 1893.

Anuradhapura District: between Ratmale and Talawa, *ca.* 7 miles SSW of Anuradhapura, *T. Koyama & Herat 13608* (NY, PDA, US). Polonnaruwa District: Minnariya Tank, *Trimen* in 1884 (PDA). Batticaloa District: Batticaloa, *Trimen C.P. 3560* (K, PDA). Hambantota District: Tissamaharama, *Trimen* in 1882 (PDA).

Distribution. North and Tropical Africa, Madagascar, India, Indo-China, Malesia and northern Australia.

37. **Cyperus pygmaeus** Rottboell, Descr. Icon. Rar. Nov. Pl. 20, *t. 14 f. 4-5* 1773; Nees in Wight, Contrib. Bot. India 72, 1834; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 18, 1900; Kern, Fl. Males. I, **7** (3): 634, 1974.

Juncellus pygmaeus (Rottb.) C. B. Clarke, Fl. Brit. India **6**: 596, 1983. ——— *Cyperus michelianus* (L.) Delile subsp. *pygmaeus* (Rottb.) Aschers. & Graebn., Synops. Mitteleur. Fl. **2** (2): 273, 1903; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 312, *f. 35 F-G,* 1936.

Polonnaruwa District: Gal Oya Reservoir, near spilway, 270 m alt., *Comanor, 561a & 561b* (NY, US). Puttalam District: Palavi Atta Villu, *Cooray* 6 Oct. 1969 (NY); Puttalam, *Trimen* Aug. 1883 (PDA). Trincomalee District: Kantalai Tank, Mile 134 on Rd. A 6, *Davidse 7518* (MO, NY). Mannar District: Aruvi Aru, Mile 125 on Rd. A 4, *T. Koyama et al. 13934B* (NY); Palavi, *Cooray* in 1969 (PDA). Anuradhapura District: Anuradhapura, *Trimen* Oct. 1883 (PDA). Matale District: Ereua Tank, *ca.* 5 miles ESE of Dambulla, 650 ft. alt., *Davidse 7391* (MO, NY, PDA, US). Colombo District: Colombo, *Ferguson C.P. 3947* (K, PDA). Hambantota District: Ruhuna National Park, Attaville, *Cooray* 6 Oct. 1969 (NY).

Distribution. Widely spread in Eurasia, from Mediterranean Region and East Africa through Asia Minor and India to southeastern Asia, Malesia and Australia.

PYCREUS P. Beauvois

1. Achenes transversely wrinkled with oblong epidermal cells .... **38** *P. stramineus*

1. Achenes smoothish to puncticulate with isodiametrical or hexagonal epidermal cells

    2. Culms few- to several-nodose below the middle, the lower part decumbent or obliquely ascending, branching and rooting at lower nodes; glumes furrowed on both sides of costa .... **39** *P. sanguinolentus*

    2. Culms not nodose above the base, erect from very base; glumes not furrowed

3. Culms 20–90 cm tall; glumes acute to subobtuse at apex, never emarginate nor cuspidate
    4. Glumes orbicular-obovate, ca. 1 mm wide in half view, the margins very broadly whitish-hyaline, rounded to apex, spikelets 3 mm wide; culms 2–3 mm thick, mostly solitary .... **40** *P. puncticulatus*
    4. Glumes ovate to lance-ovate, ca. 0.5 mm wide in half view, hardly or very narrowly hyaline on margins, acute at apex; spikelets ca. 1.5 mm wide; culms 0.7–2 mm thick, as a rule tufted
        5. Lowest bract as long as to at most 2.5 times as long as the umbel, when longer than that, then inflorescence congested in a head; spikelets rusty brown to yellowish brown .... **41** *P. polystachyos*
        5. Lowest bract 3 to 5 times as long as the umbel; spikelets dark purplish-brown to chestnut-brown .... **42** *P. flavidus*
3. Culms 1–8 cm tall; glumes truncate to emarginate at apex, the midvein excurrent beyond the glume apex into a recurved mucro
    6. Glumes ovate, close together not exposing achenes; rays normally poorly developed .... **43a** *P. pumilus* ssp. *pumilus*
    6. Glumes oblong to lance-oblong, spaced, so that achenes exposed between glumes; rays well developed .... **43b** *P. pumilus* ssp. *membranaceus*

38. **Pycreus stramineus** (Nees) C. B. Clarke, Fl. Brit. Ind. **6**: 589, 1893; Alston in Trimen & Hook. f., Handb. Fl. Ceylon **6**: 306, 1931.

Cyperus stramineus Nees in Wight, Contrib. Bot. India 74, 1834; Trimen, Handb. Fl. Ceylon **5**: 19, 1900. Not of Desf. ex Link, 1820. ——— *Cyperus substramineus* Kükenthal, Pflanzenr. **4** (20), 101 Heft: 398, 1936; Kern, Fl. Males. Ser. 1, **7** (3): 653, 1974.

Kurunegala District: Kurunegala, *Trimen C.P. 3776* (PDA).

Distribution. India, Ceylon, Indo-China and Malay Peninsula.

Thus far known from Ceylon by a single collection only. This species closely resembles *P. flavescens* of much wider distribution, from which it differs primarily in its longer spikelets that are 8 to 35 mm long bearing many acute-tipped glumes in contrast to shorter spikelets (6 to 10 mm in length) with several obtuse glumes in the latter.

39. **Pycreus sanguinolentus** (Vahl) Nees [Linnaea **9**: 283, 1835. Invalid combination] ex C. B. Clarke, Fl. Brit. India **6**: 590, 1893; C. E. C. Fischer in Gamble, Fl. Presid. Madras **9**: 1627, 1931; Alston in Trimen & Hook. f., Handb. Fl. Ceylon **6**: 307, 1931.

Cyperus sanguinolentus Vahl, Enum. Pl. **2**: 351, 1806; Nees in Wight, Contrib. Bot. India 75, 1834; Thwaites, Enum. Pl. Zeyl. 342, 1864; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 20, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 385, 1936; Kern, Fl. Males. Ser. 1, **7** (3): 646, 1974. ——— *Cyperus eragrostis* Vahl, Enum. Pl. **2**: 322, 1806; Trimen, Syst. Cat. Flow. Pl. & Ferns Ceylon 99, 1885. Not of Lamarck, 1791.

Wilpattu National Park: Manikepola Uttu, *T. Koyama et al. 13460* (NY, PDA, US). Kandy District: Peradeniya, near water fall above University campus, *Comanor 690* (NY): *ca.* 5 miles S.E. of Gampola, at Mile 18/6 on Gampola-Nuwara Eliya Rd., 720 m alt., *Davidse et al. 7924* (MO, NY). Ratnapura District: 11 miles E. of Diniyaya on Rd. A17, 750 m alt., *Davidse 7586* (MO, NY). Amparai District: Senanaike Samudra, Padagoda, *T. Koyama et al. 13983* (NY, PDA, US).

Fig. 7. *Pycreus puncticulatus* (Vahl) Nees. *A*, habit. *B* & *C*, two views of prophyll. *D*, spikelet. *E*, portion of rhachilla with two flowers. *F*, glume. *G*, lateral view of achene. Scales = 1 mm.

Rather widely distributed in the Old World from northeastern Africa through Afghanistan, India and Indo-China northeastwards to China and Japan, eastwards to Malesia.

40. **Pycreus puncticulatus** (Vahl) Nees, Fl. Brasil. **2** (1): 10, in note, 1842; C. B. Clarke, Fl. Brit. India **6**: 593, 1893; C. E. C. Fischer in Gamble, Fl. Presid. Madras **9**: 1628, 1931; Alston in Trimen & Hook. f., Handb. Fl. Ceylon **6**: 307, 1931. ——— **Fig. 7**.

Cyperus puncticulatus Vahl, Enum. Pl. **2**: 348, 1806; Thwaites, Enum. Pl. Zeyl. 342, 1864; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 21, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 362, 1936. ——— *Cyperus baccha* Kunth, Enum. Pl. **2**: 115, 1837. ——— *Pycreus baccha* (Kunth) Nees, [Linnaea **9**: 283, 1835. Invalid combination] Fl. Brasil. **2** (1): 10, 1842. In note.

Trincomalee District: Mavadichchenai, *Alston 544* (PDA); Trincomalee, *Glenie C.P. 3751* in part (PDA). Matale District: Dambulla, *Thwaites C.P. 3751* (K, PDA). Kurunegala District: Kurunegala, *Ranasinghe 843* (PDA). Galle District: Haburagala, *Amaratunga 2315* (PDA). Amparai District: E of Kunukala Kalapuwa Lagoon, *ca.* 4 miles S of Panama, sea level, *T. Koyama et al. 14027* (NY, PDA, US); Helawe Eliya, *ca.* 7 miles S of Panama, E of Helawe Lagoon, sea level, *T. Koyama et al. 14025* (NY, PDA, US). Ruhuna National Park: Uraniyawala, *ca.* 1 mile W of Buttawa, *Fosberg et al. 51018* (US); Palugaswela, Ecology Project Block I, *Cooray* 23 Mar. 1970 (NY).

Distribution. Rather sporadically noted from southern India (Bombay, Mysore and Madras), Malay Peninsula and Cochinchina.

In the genus *Pycreus* this species is well demarcated by its relatively loose, large umbel with broad, red-brownish spikelets, in which it resembles superficially *Cyperus procerus*, a stoloniferous perennial with trigonous achenes.

41. **Pycreus polystachyos** (Rottboell) P. Beauvois, Fl. d'Oware **2**: 48, *t. 86, f. 2,* 1807; C. B. Clarke in Hook. f., Fl. Brit. India **6**: 592, 1893; Alston in Trimen & Hook. f., Handb. Fl. Ceylon **6**: 307, 1931.

Cyperus polystachyos Rottboell, Descr. Icon. Rar. Nov. Pl. Illustr. 39, *t. 11, f. 1,* 1773; Nees in Wight, Contrib. Bot. India 75, 1834; Thwaites, Enum. Pl. Zeyl. 342, 1864; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 20, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 367, 1936; Kern, Fl. Males. Ser. 1, **7** (3): 649, 1974. ——— *Cyperus paniculatus* Rottboell, Descr. Icon. Rar. Nov. Pl. Illustr. 40, 1773. ——— *Pycreus paniculatus* (Rottb.) Nees [Linnaea **9**: 283, 1835. Invalid combination] ex Alston in Trimen & Hook. f., Handb. Fl. Ceylon **6**: 307, 1931. ——— *Cyperus polystachyos* Rottb. var. *laxiflorus* Bentham, Fl. Austral. **7**: 261, 1878; Kükenthal, Pflanzenr. **4** (20), Heft. 101: 370, 1936. ——— *Pycreus polystachyos* P. Beauv. var. *laxiflorus* (Bentham) C. B. Clarke, Fl. Brit. India **6**: 592, 1893.

Jaffna District: Jaffna, *Ferguson C.P. 800* (PDA). Anuradhapura District: Anuradhapura, *Alston 638* (PDA). Wilpattu National Park: Kuda Patessa, *Wirawan et al. 1035* (US); Kollankanatta, *Mueller-Dombois et al.* 27 Apr. 1969 (US); N.E. of Kuruttu Pondi Villu, *T. Koyama 7560* (NY). Trincomalee District: Trincomalee, *Glenie C.P. 800* (PDA); Ottawady, valley of downstream of Mahaweli Ganga, *ca.* sea level, *T. Koyama 13652* (NY, PDA, US); Mile 97 on Rd. A 15, *Davidse 7560* (MO, NY). Polonnaruwa District: *ca.* 1 mile NE of Elahera along Amban Ganga, 400 ft. alt., *Davidse 7357* (MO, NY). Batticaloa District: Batticaloa, *Thwaites C.P. 800,* March 1868 (K, PDA). Nuwara Eliya District: Ramboda Rd., near Ramboda, 3200 ft., *Ballard 1136* (K, NY); Maskeliya, *Wright* 11 Nov. 1926 (PDA). Matale District: Bata-Anduwa Gap, Sevastine, at marker 34/6, 1300 m alt., *Tirvengadum et al. 17* (PDA). Kandy District: Hantane, *Silva 296* (PDA); Peradeniya, *Alston 280* (PDA); Gampola-Dolosbage Rd., *Grupe 159* (PDA).

Kurunegala District: Kurunegala, *Thwaites C.P. 800* (PDA); Beddegama, *Alston 1397* (PDA). Colombo District: Muturajawela, *Amaratunga,* 18 Jan. 1971 (PDA). Galle District: Horawala, left bank of Bentota Ganga, *Amaratunga 2495* (PDA), Haburagola, *Amaratunga 2381* (PDA). Amparai District: Tandiadi Kalapu Lagoon, S of mile 215 on Road A4, *T. Koyama et al. 14018* (NY, PDA, US); 3 miles NW of Maha Oya, 50 m alt., *Davidse et al. 9008* (MO, NY,); Inginiyagala National Park, between Baduluwela and "Westminster Abeey", *T. Koyama et al. 13995* (PDA). Ruhuna National Park: Uraniya, Ecology Project Block I, *Cooray* 22 Mar. 1970 (PDA, US).

Distribution. Cosmopolitan, tropical and subtropical regions. The range is extending into warm-temperate regions in eastern Asia as far as to central Japan, and into Mediterranean Region.

This species is extremely variable in the color of spikelets and in the inflorescences, which vary from a rather open umbel with spicately disposed spikelets to a head through an intermediate state bearing fascicled spikelets on short rays. In Ceylon plants with open inflorescences are common. Although Alston (in Trimen & Hook. f., Handb. Fl. Ceylon 6: 307, 1932) listed *P. ferrugineus* as occurring in Ceylon without citation of specimens, I have so far been unable to see any documentation of this essentially African species from Ceylon and India. *Pycreus ferrugineus* distinctly differs from *P. polystachyus* at least in its spreading spikelets that are much broader than those of the latter at 2 to 3 vs. 1.25 to 1.5 mm in width, and it can no way be confused with the latter. Hence, Alston's note under *P. ferrugineus* mentioning that "This is doubtfully distinct from *P. polystachyus,*" and "Up to 5000 ft.; common" implies that his *P. ferrugineus* may constitute a misidentification for *P. polystachyos* itself.

42. **Pycreus flavidus** (Retzius) T. Koyama, Journ. Jap. Bot. **51** (10): 313, 1976.

Cyperus flavidus Retzius, Obs. Bot. **5**: 13, 1788; Vahl, Enum. Pl. **2**: 334, 1806; Kern, Fl. Males. Ser. 1, **7** (3): 648, 1974. ——— [*Cyperus globosus* Allioni, Auctuar. Fl. Pedemont. 49, 1789; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 21, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 352, 1936. Not of Forskael, 1775.] ——— *Cyperus strictus* Roxburgh, Fl. Ind. ed. 1, **1**: 203, 1820. ——— *Cyperus capillaris* König ex Roxburgh, l.c. **1**: 198, 1820; Nees in Wight, Contrib. Bot. Ind. 76, 1834. ——— *Pycreus globosus* (Allioni) Reichenbach, Fl. Germ. Excurs. 140, 1830. ——— *Pycreus capillaris* (König ex Roxb.) Nees [Linnaea **9**: 283, 1834. Invalid combination] ex C. B. Clarke, Fl. Brit. India **6**: 591, 1893. ——— *Pycreus strictus* (Roxb.) Alston in Trimen & Hook. f., Handb. Fl. Ceylon **6**: 307, 1931. ——— "*Cyperus flavescens* L." sensu Thwaites, Enum. Pl. Zeyl. 342, 1864.

Polonnaruwa District: *ca.* 1 mile N.E. of Amban Ganga, 400 ft. alt. *Davidse* 7357A (MO). Kandy District: *ca.* 5 miles SE of Gampola at mile 18/6 on Road A5, 720 m alt., *Davidse et al. 7925* (MO, NY); *ca.* 2 miles E. of Maddakele, slope N.W. of Krinckles, 1440 m alt., *Davidse 8332* (MO); Pallekale, *Alston 278* (PDA); Gordindihela, *Willis,* 27 Feb. 1906 (PDA); Upper Hantane Rd., above the University Campus, *Comanor 317* (PDA, US). Kurunegala District: Kurunegala, *Gardner C.P. 801* (PDA). Nuwara Eliya District: Nuwara Eliya, *Trimen C.P. 801* (PDA), *Amaratunga 230 & 1305* (PDA); Pattipola, *Lazarides 7291* (PDA, US); between Hakgala and Nuwara Eliya, 5400 ft., *Ballard 1269* (K, NY); Corbett's Gap, 4000 ft., *Ballard 1050* (K, NY); Moon Plains, 6000 ft., *Ballard 1217A* (K, NY). Ratnapura District: 11 miles E of Deniyaya at mile 62 on Rd. A17, 750 m alt., *Davidse 7884* (MO, NY); Ratnapura, *Thwaites C.P. 801* (K, PDA). Colombo District: Mount Lavinia, *Trimen* Oct. 1881 (PDA). Monaragala District: *ca.* 3 miles W. of Wellawaya at mile 135/10 on Rd. A4, 990 ft., *Davidse 7742* (MO, NY). Ruhuna National Park: Kumbukkan Oya, Ecology Project Block II, *Cooray* 31 July 1969 (NY, US). Hambantota District: 2 miles E of Katuwana, *Lazarides 7350* (PDA, US).

Widely distributed from Mediterranean Region and tropical Africa eastwards to Central and southern Asia, and northeastwards to Japan.

This widespread species is variable particularly in the width and the color of spikelets. Ceylonese plants from up countries at altitudes of over 750 m generally possess strongly compressed, dark purplish-brown spikelets that are mostly less than 1.5 mm in width, a form resembling plants from Japan and temperate India. A few specimens collected at low altitudes such as *Cooray* 31 July 1969 and *Davidse 7357A* cited above bear less compressed, broader spikelets with stramineous-brown scales.

43. **Pycreus pumilus** (L.) Nees [Linnaea **9**: 283, 1935. Invalid combination] ex C. B. Clarke, Fl. Brit. India **6**: 591, 1893, concerning the nomenclature, but excluding basionym; Domin, Bibl. Bot. Heft. **85**: 417, 1915; C. E. C. Fischer in Gable, Fl. Madras **9**: 1627, 1931.

Cyperus pumilus L., Cent. Pl. **2**: 6, 1756; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 19, 1900; Kükenthal, Pflanzenr. **4** (20), Heft. 101: 375, *f. 44 A-E*, 1936; Kern, Fl. Males. Ser. 1, **7** (3): 650, f. 66, 1974. ——— *Cyperus pluvinatus* Nees & Meyen in Wight, Contrib. Bot. India 74, 1834; Thwaites, Enum. Pl. Zeyl. 342, 1864. ——— *Pycreus nitens* Nees, Nova Acta Nat. Cur. **19**, Suppl. **1**: 53, 1843; C. B. Clarke, Fl. Brit. India **6**: 591, 1893. ——— *Pycreus pulvinatus* (Nees & Meyen) Nees & Meyen ex Nees [Linnaea **9**: 283, 1835, invalid combination, &] Nova Acta Nat. Cur. 19, Suppl. **1**: 53, 1843. ——— *Dichostylis nitens* (Nees) Palla, Bot. Jahrb. **10**: 296, 1889. ——— "*Pycreus patens* (Vahl)" sensu Alston in Trimen & Hook. f., Handb. Fl. Ceylon **6**: 306, 1931. Invalid combination.

43a. Subsp. **pumilus.**

Jaffna District: Jaffna Lagoon, north shore at *ca.* 10 miles SE of Navatkuli, *T. Koyama et al. 14040* (NY, PDA, US); Jaffna, *Gardner* in 1846 (PDA). Anuradhapura District: Maradaukadewela, *Trimen* 21 Jan. 1896 (PDA); Wilpattu National Park, East Intermediate Zone, along Wildlife Dept. path at *ca.* 2 miles from barrier gate, *T. Koyama & Jayasuria 13966* (NY, PDA, US). Polonnaruwa District: Tamankaduwa, *Townsend 73/250* (K, US). Trincomalee District: Periya Kulam, *ca.* 7 miles NW of Trincomalee, *T. Koyama* et al. *14064* (NY, PDA, US); Trincomalee, west side of Welcomble Hotel, *Wheeler 12411* (PDA). Mannar District: Aruvi Aru, mile 125 on Rd. A14, *T. Koyama et al. 13931* (NY, PDA, US). Puttalam District: Chilaw, *Trimen,* Dec. 1880 (PDA). Kandy District: Peradeniya, *Thwaites C.P. 806* in part (PDA); Gannoruwa, *Alston 298* (PDA); Haragama, *Alston* 3 Oct. 1926 (PDA).

Distribution. From India through Indo-China and southern China eastwards to Malesia and Australia (rare in Queensland).

Alston (l.c., 1931) applied *Cyperus patens* Vahl to the Ceylonese plants then passing as *Cyperus pumilus,* and proposed a combination, *Pycreus patens* (Vahl). Typical *C. patens* from Africa closely resembles subsp. *membranaceus,* and it may not be sufficiently different from the latter. However, *C. patens* without doubt does not represent the common phase of Ceylonese *C. pumilus.*

43b. Subsp. **membranaceus** (Vahl) T. Koyama, *stat. nov.*

Cyperus membranaceus Vahl, Enum. Pl. **2**: 330, 1806. ——— *Cyperus nitens* Retz. var. *membranaceus* (Vahl) Böckeler, Linnaea **35**: 484, 1868. ——— *Cyperus pumilus* L. var. *membranaceus* (Vahl) Kükenthal, Pflanzenr. **4** (20), 101 Heft: 376, 1935. ——— *Cyperus pumilus* L. forma *membranaceus* (Vahl) C. B. Clarke, Journ. Linn. Soc. **21**: 44, 1884.

Hambantota District: Ruhuna National Park, between the Entrance and Ecology Project Plot R9, *Cooray s.n.,* 11 Dec. 1969 (NY, US); Uraniya, *Cooray,* 22 Mar. 1970 in part (NY).

Distribution. India, Ceylon and Thailand; rather frequent in southern India, but rare in Thailand.

Cooray's record, cited above, makes a new entry of subsp. *membranaceus* to the flora of Ceylon. The difference between subsp. *membranaceus* and the typical phase exists mainly in the relatively minor details of floral glumes and achenes. In subsp. *membranaceus* the oblanceolate to oblong-obovate glumes are only ca. 1/3 mm wide in half view, being broadest much above the middle, and are considerably loosely disposed on the rhachilla exposing the greater portion of achenes between the glumes just as in *Cyperus tenuispica,* whereas in subsp. *pumilus* its broader elliptic to ovate-elliptic glumes are 1/2 to 3/5 mm wide in half view being broadest just below the middle, and are closely arranged, there being no space between two glumes. In general, the achenes of subsp. *membranaceus* are truly obovate and cannot be seen through the membranous glumes, while in subsp. *pumilus* its elliptic to lance-elliptic achenes are usually seen through the hyaline glumes. The spikelets of subsp. *membranaceus* are shorter and more laxly disposed on well elongated rays in contrast to the usually more congested nearly head-like inflorescence in subsp. *pumilus*. Though minute, these differances are sufficiently consistent as far as I have examined materials, and hence I regard subsp. *membranaceus* a valid taxon.

MARISCUS Gaertner

1. Spikelets more or less flattened with acute edges, bearing 3 to many achenes; glumes folded with a conspicuous keel, laxly holding achene
    2. Plants perennial; culms more than 50 cm tall; leaves septate-nodulose; glumes without recurved awn
        3. Spikelets lanceolate, 2 mm wide, straw-coloured, disposed in a spike .... **44** *M. javanicus*
        3. Spikelets linear, 1 mm wide, reddish-brown, densely congested in a globose head .... **45** *M. compactus*
    2. Plants annual; culms 4–20 cm tall; leaves not septate-nodulose; glumes with recurved awn, heance spikelets squarrose .... **46** *M. squarrosus*
1. Spikelets terete without conspicuous edges, bearing 1 or 2 achene(s) only; glumes involute without distinct keel, tightly surrounding achene
    4. Rhachilla slender, not at all spongy-thickened; spikelets 1- or 2-fruited
        5. Base of culms hardly enlarged or slightly globose with a corm-like enlargement; basal leaf sheaths purplish-brown
            6. Spikelets mostly 2-fruited, greenish to greenish-straw-coloured, patent to ascending at maturity, mostly 4–5 mm long; achenes 2 mm long
                7. Spikes umbellate with elongated rays; spikelets spreading or the lower ones weakly reflexed at maturity .... **47** *M. sumatrensis*
                7. Spikes subsessile, nearly capitate; spikelets at least the lower ones obliquely patent at maturity
                    8. Rhizome short, not stoloniferous; leaves 2–5 mm wide; umbel truly terminal .... **48a** *M. cyperinus* ssp. *cyperinus*
                    8. Rhizome emitting slender stolons; leaves as a rule 0.7–1 mm wide; umbel quasi-lateral with the lowest bract continued down to the culm .... **48b** *M. cyperinus* ssp. *laxatus*

6. Spikelets 1-fruited, whitish-green, spreading at maturity, mostly 2–3 mm long; achenes ca. 1.3 mm long .... **49** *M. paniceus*

5. Base of culm quasi-bulbose, i.e., with an ovoid to ovoid-oblong thickening clothed with leaf sheaths; basal leaf sheaths straw-brown.

9. Rhizome emitting slender stolons; spikes sessile yet recognizable. .... **50** *M. clarkei*

9. Rhizome loosely tufted without stolons; spikes congested in an ovoid or conical head, not readily recognizable .... **51** *M. dubius*

4. Rhachilla spongy-thickened; achenes sunken in a depression of spongy rhachilla-internodes; spikelets 1-fruited .... **52** *M. pedunculatus*

44. **Mariscus javanicus** (Houttuyn) Merrill & Metcalfe, Lingnan Sci. Journ. **21**: 4, 1945.

Cyperus javanicus Houttuyn, Nat. Hist. II, 13 Aanw. Pl. (1), *t. 88 f. 1*, 1782; Kern, Fl. Males. I, **7** (3): 635, *f. 63*, 1974. —— *Cyperus pennatus* Lamarck, Illustr. **1**: 144, 1791; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 476, *f. 53 A-G*, 1936. —— *Mariscus albescens* Gaudichaud in Freyc., Boy. Bot. 415, 1826; C. B. Clarke, Fl. Brit. India **6**: 623, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 40, 1900. —— *Mariscus pennatus* (Lamarck) Domin, Bibl. Bot. Heft. **85**: 440, 1915.

Wilpattu National Park: Manikepola Uttu, *T. Koyama 13456* (NY, PDA, US). Anuradhapura District: Ritigala Strict Natural Reserve, approach to Weweltenna along southern slope, 700 ft. alt., *Jayasuria 1294* (PDA); Anuradhapura, *Trimen* in 1881 (PDA). Trincomalee District: Mile 79 on Road A 4, *Davidse 7558* (MO, NY). Batticaloa District: Batticaloa, *Trimen C.P. 678* p.p. (PDA, K). Monaragala District: Crossing of Rd. A 2 and Kirindi Oya at Mile 183/2, *ca.* 15 miles S of Wellawaya, 400 ft. alt., *Davidse 7760* (MO, NY, PDA, US). Ratnapura District: Raigam Korale, *Thwaites C.P. 678* p.p. (PDA). Galle District: Bentota, *Ballard 1507* (K, NY). Hambantota District: N of Kataragama, *Wirawan 644* (PDA); Ruhuna National Park: Block 3, *Cooray* 23 May 1968 (PDA, US).

Distribution. Tropical Africa, Madagascar through Indian Subcontinent to southern China and the southern Ryukyus, as well as to Malesia, northern Australia and the Pacific Islands.

45. **Mariscus compactus** (Retzius) Boldingh, Zakfl. Landb. Java 77, 1916; Druce, Rep. Bot. Exch. Club Brit. Isls. 1916: 634, 1917; Fischer in Gamble, Fl. Madras **9**: 1645, 1931. ———— **Fig. 8**

Cyperus compactus Retzius, Osb. Bot. **5**: 10, 1789; Kükenthal, Pflanzenr. **4** 20), 101 Heft: 423, 1936; Kern, Fl. Males. I, **7** (3): 638, 1974. ——— *Cyperus dilutus* Vahl, Enum. Pl. **2**: 357, 1806. —— *Mariscus microcephalus* Presl. Reliq. Haenk. **1**: 182, 1828; C. B. Clarke, Fl. Brit. India **6**: 624, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 40, 1900. —— *Mariscus dilutus* (Vahl) Nees in Wight, Contrib. Bot. India 90, 1834.

Badulla District: ca. 8 miles E of Mahiyangana, 3.5 miles N of Mile 53 on Mihiyangana-Padiyatalawe Rd., *T. Koyama et al. 13979* (NY, PDA, US).

Distribution. India, southern continental China, Taiwan and Malesia.

This species, easily recognizable by its characteristic globose spikes, occurs very sporadically in the low countries in Ceylon. I have not seen Gardner's collection from Kornegalle, which was cited by both Thwaites and Trimen as *C.P. 815*, and which seems to be the only other documentation of this species from Ceylon.

46. **Mariscus squarrosus** (L.) C. B. Clarke, Fl. Brit. India **6**: 623, 1893, concerning the basionym.

Cyperus squarrosus L., Cent. Pl. **2**: 6, 1756; Kern, Fl. Males. I, **7** (3): 631, 1974. ——— *Cyperus aristatus* Rottboell, Descr. Pl. Rar. Progr. 22, 1772; C. B. Clarke, Fl. Brit. India **6**: 606, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 24, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 502, *f. 55 F-J*, 1936. ——— *Mariscus aristatus* (Rottboell) Chermezon, Bull. Soc. Bot. France **85**: 366, 1938; Tang & Wang, Fl. Reipubl. Pop. Sin. **11**: 178, *pl. 59*, 1961.

Jaffna District: north shore of Jaffna Lagoon, *ca.* 10 miles SE of Navatkuli, sea level, *T. Koyama et al. 14037* (NY, PDA, US); Keerimalai to Point Pedro, *Clayton 5205* (K). Wilpattu National Park: near Sadpuda Kallu, 2 miles E of Kattankandal Kulam, 30 m alt., *Fosberg et al. 50830* (NY, US). Trincomalee District: Trincomalee, *Glenie C.P. 966* ex p. (PDA). Puttalam District: Puttalam, *Ferguson* in 1881 (PDA). Polonnaruwa District: Polonnaruwa, *Clayton 5116* (K, PDA); 13 miles E of Polonnaruwa on Trincomalee Rd., *Clayton 5135* (K, PDA); *ca.* 1 mile E of Kolakanaweli, Mile 56/7 on Batticaloa Rd., *T. Koyama 13575* (NY). Mannar District: Aruvi Aru, Mile 125 on Rd. A 14, *T. Koyama et al. 13934* (NY, PDA, US). Anuradhapura District: Galpitigala, a few miles from Ritigala, *Ballard 1451* (K, NY). Vavunia District: Palayanalankulan, Mile 120 on Rd. A 14, *T. Koyama et al. 13938* (NY, PDA, US). Kandy District: Hantane, *Thwaites C.P. 966* (K, PDA); Giragama, *Amaratunga 359* (PDA). Hambantota District: Tissamaharama, *Trimen* Dec. 1882 (PDA); Rhuhuna National Park, Kohombagaswala, Block I, *Cooray et al.* 22 Jan. 1969 (US); Uraniya, *Cooray* 22 Mar. 1970.

Distribution. Widely distributed in tropical and subtropical regions of the world, extending also into temperate regions in the Americas, where the range covers from southern Canada south to Argentina and Chile. In Ceylon common on wet sandy soil in open grasslands.

In the Linnaean Herbarium the specimen marked as "*squarrosus*" in Linnaeus' hand represents this taxon, while the second sheet with a single inflorescence is *Cyperus maderaspatanus*. Consequently, *Cyperus squarrosus* is the correct name of what has generally been called *C. aristatus*. Although I place this species in *Mariscus* following Chermezon and Wang & Tang (locis cit.), as was already pointed out by O'Neill (Rhodora 44: 47, 1942) and Kern (op. cit.) the caducity of the rhachillas of this species is not constant. In Ceylonese specimens I noticed in a few specimens that the glumes fall off apart from the rhachilla, which eventually falls off the rhachis. This species, which is characteristically intermediate between *Cyperus* and *Mariscus*, requires more detailed anatomical studies which might elucidate the systematic link between the two genera.

47. **Mariscus sumatrensis** (Retzius) T. Koyama, *comb. nova*

Scirpus cyperoides L., Mant. **2**: 181, 1771. ——— [*Kyllinga umbellata* Rottboell, Descr. Icon. Rar. Nov. Pl. 15, 1773, excluding *t. 4 f. 2.* Illegitimate name.] ——— *Kyllinga sumatrensis* Retzius, Obs. Bot. **4**: 13, 1786. ——— *Kyllinga umbellata* Rottb. var. *sumatrensis* (Retz.) Willdenow, Sp. Pl. **1**: 258, 1797. ——— [*Mariscus umbellata* (Rottb.) Vahl, Enum. **2**: 376, 1806. Combination based on illegitimate name.] ——— *Mariscus sieberianus* Nees [Linnaea **9**: 286, 1835, nomen nudum] ex C. B. Clarke, Fl. Brit. India **6**: 622, 1893, & Illustr. Cyper. *t. 23 f. 5-6*, 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 42, 1900. ——— *Mariscus cyperoides* (L.) Urban, Symb. Antill. **2** (1): 164, 1900. Not of Dietrich, 1833. ——— *Cyperus cyperoides* (L.) O. Kuntze, Rev. Gen. Pl. **3** (2): 333, 1898; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 514, 1936; Kern, Fl. Males. I, **7** (3): 642, 1974.

Nuwara Eliya District: Hakgala, *Alston 633* (PDA), *Mueller-Dombois* May 1968 (PDA, US); Talawakele, *Bond* 17 Feb. 1944 (PDA).

Distribution. Tropical Africa, tropical and subtropical Asia, Malesia, northern Australia; also introduced to the West Indies. In Ceylon rarely found in up countries.

Fig. 8. *Mariscus compactus* (Retzius) Boldingh. *A*, habit. *B*, orifice of a cladoprophyll at the base of umbel ray. *C*, spikelet. *D*, prophyll. *E*, lateral view of two glumes showing their base forming the wings on the rhachilla. *F*, glume. *G*, fruiting pistil. *H*, achene. Scales = 1 mm.

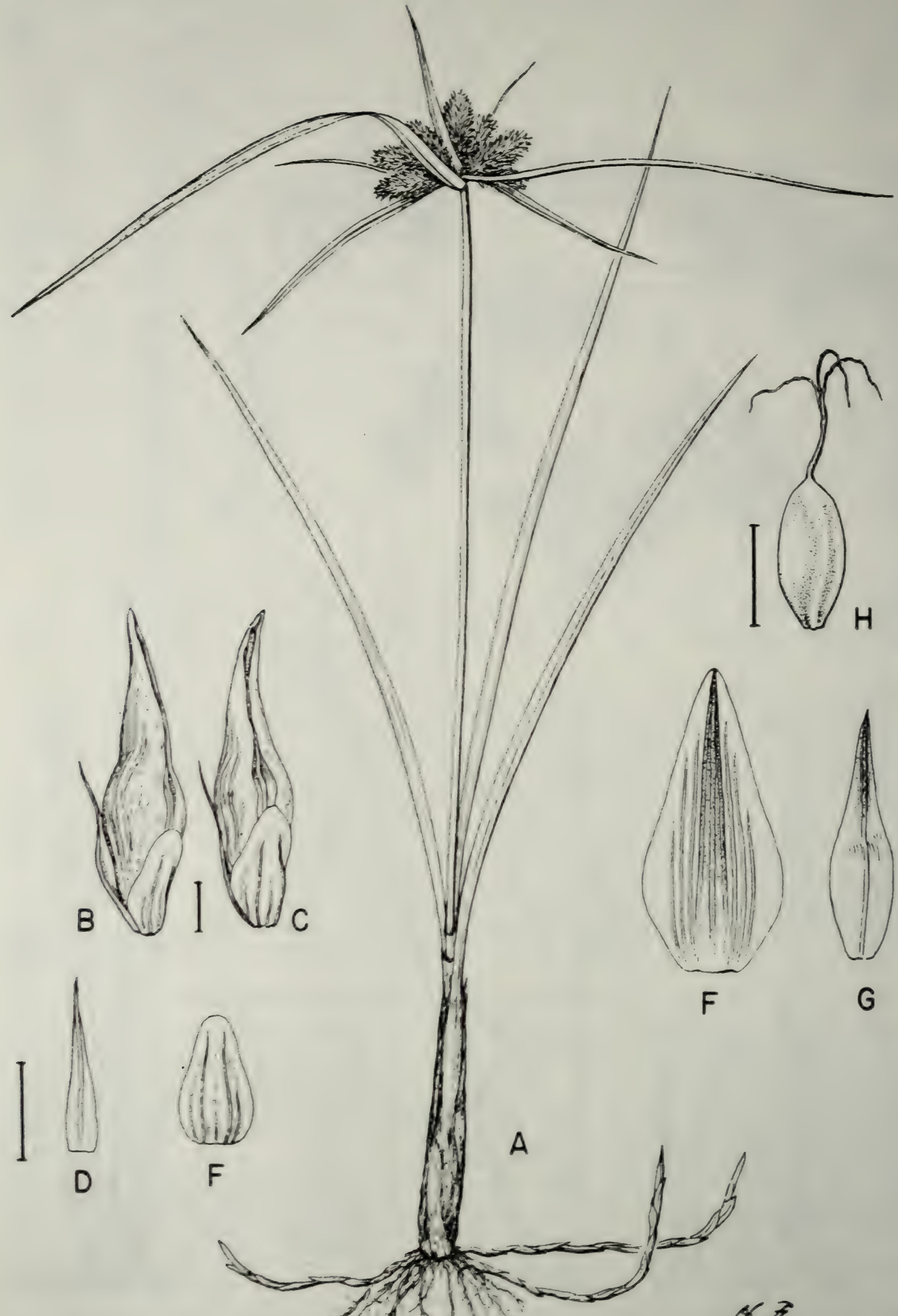

Fig. 9. *Mariscus clarkei* (T. Cook) T. Koyama. *A*, habit. *B* & *C*, two views of spikelet. *D*, bracteole subtending a spikelet. *E*, prophyll. *F*, fruiting glume. G, empty glume. *H*, achene. Scales = 1 mm.

When this taxon is placed in *Mariscus,* its earliest valid name, *Scirpus cyperoides,* cannot be transfered because of Dietrich's homonym. Next earliest name, *Kyllinga umbellata,* is illegitimate since Rottboell cited *Scirpus cyperoides* in the synonymy. *Kyllinga sumatrensis,* therefore, needs to be transferred to *Mariscus* to form the correct name of this species under the genus.

48. **Mariscus cyperinus** (Retzius) Vahl, Enum. Pl. **2**: 377, 1806; C. B. Clarke, Fl. Brit. India **6**: 621, 1893, & Illustr. Cyper *t. 12 f. 3-4,* 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 42, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1644, 1931.

Kyllinga cyperina Retzius, Obs. Bot. **6**: 21, 1791. ——— *Cyperus cyperinus* (Retzius) Suringar, Het. Gesl. Cyper. Mal. Archip. 154, *t. 6 f. 10,* 1898; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 518, 1936; Kern, Fl. Maels. I, **7** (3): 641, 1974.

48a. Subsp. **cyperinus.**

Ceylon: without definite locality, *Trimen C.P. 816* (PDA). Kandy District: *ca.* 2 miles N of Hunnasgiriya, near Mile 23, 380 m alt., *Davidse 8457* (MO, NY); Pusselawa, *Alston 1170* (PDA); Peradeniya, *Thwaites C.P. 816* (K, PDA), *Amaratunga 643* (PDA), *Alston 593* (PDA); Morakande Estate, *Alston 594* (PDA); Gannoruwa, *Alston 851* (PDA); Gampola, *Alston 592* (PDA). Matale District: 33/7 Midlands, 1200 m alt., *Tirvengadum et al. 14* (US); Matale, *Tirvengadum et al. 16* (PDA). Nuwara Eliya District: Ramboda Pass, 3200 ft. alt., *Ballard 1142A* (K, NY). Badulla District: Rawanaella Waterfall, *ca.* 2 miles SE of Ella, 750 m alt., *Davidse et al. 8868* (NY, PDA, US). Colombo District: Dewalgama, *Amaratunga 1162* (PDA); Ekala, *Alston 2389* (PDA).

Distribution. From India to Malesia and northern Australia, also in Eastern Asia extending northwards to southern China and the Ryukyus. Open grassy places in hilly countries.

48b. Subsp. **laxatus** (C. B. Clarke), T. Koyama, *stat. nov.*

Cyperus umbellatus C. B. Clarke var. *laxatus* C. B. Clarke, Journ. Linn. Soc. **21**: 201, 1888. ——— *Cyperus cyperinus* Suringar forma *curvata* Suringar, Het Gesl. Cyper. Mal. Archip. 156, 1898; Kern, Fl. Males. I, **7** (3): 624, 1974. ——— *Mariscus tenuifolius* Schrader ex Nees, Fl. Brasil. **2** (1): 46, 1842; C. B. Clarke, Fl. Brit. India **6**: 622, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 43, 1900; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1644, 1931.

Kandy District: Hunnasgiriya, collector unknown 590 (PDA); Peradeniya, *Alston 387* (PDA), *Thwaites C.P. 817,* ex p. (PDA); Maturata, *Thwaites C.P. 817* ex p. (PD). Matara District: Weligama, *Alston 1172* (PDA). Monaragala District: *ca.* 3 miles W of Wellawaya, near Mile 135/10, 990 ft. alt., *Davidse 7741* (MO, NY). Ruhuna National Park: Ecology Project Prot R19, *Cooray* 11 Dec. 1969 (US).

Distribution. India to Malesia; not as common as the typical phase.

Subspecies *laxatus* differs from the typical phase in its narrow habit with long-creeping slender stolons and the few-spiked contracted umbels that tend to become pseudo-lateral being subtended by the lowest leafy bract continued down to the culm. As far as the Ceylonese plants are concerned this combination of characters appears to be rather constant, on which basis I regard this slender phase to be a subspecies of *M. cyperinus.*

49. **Mariscus paniceus** (Rottboell) Vahl, Enum. Pl. **2**: 373, 1806; C. B. Clarke, Fl. Brit. India **6**: 620, 1893, incl. var. *roxburghianus,* & Illustr. Cyper. *t. 22 f. 1-2,* 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 41, 1900, incl. var. *roxburghianus.*

[*Schaenoides paniceus* Rottboell, Descr. Pl. Rar. Progr. 15, 1772, provisional name.] ——— *Kyllinga panicea* Rottboell, Descr. Icon. Rar. Nov. Pl. 15, *t. 4 f. 1*, 1773. ——— *Cyperus paniceus* (Rottboell) Böckeler, Linnaea **36**: 381, 1870, in part, incl. basionym; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 526, 1936; Kern, Fl. Males. I, **7** (3): 643, 1974.

Anuradhapura District: Ritigala Nature Reserve, 2400 ft. alt., *Jayasuria 1710* (NY, PDA). Mannar District: Aruvi Aru, Mile 125 on Rd. A 4, *T. Koyama et al. 13928* (NY, PDA, US). Polonnaruwa District: SE of Giritale Wewa, 7 miles N.W. of Polonnaruwa, *Fosberg & Ripley 51935* (US); Polonnaruwa, *Ripley 339* (PDA); Galoya Reservoir, near spilway, 270 m alt., *Commanor 568* (NY). Nuwara Eliya District: Ramboda Pass, 3200 ft., *Ballard 1142A* (K, NY); Hakgala Botanic Gardens, *Clayton 5783* (K, PDA); between Pusselawa and Ramboda, at Mile 32/8 on N. Eliya Rd., 1100 m alt. *T. Koyama & Herat 13613* (NY, PDA, US). Matale District: *ca.* 8 miles ESE of Dambulla, *ca.* 900 ft. alt., *Davidse 7433* (MO, NY). Kandy District: Hantane, *Thwaites C.P. 814* (K, PDA); Hewaheta, *Thwaites C.P. 2878* (PDA); Maragala, *Alston 1629* (PDA); Haragama, *Alston 306* (PDA); Aladeniya, *Amaratunga 644* (PDA); between Alagalla and Balana Rd., *Comanor 440* (PDA, US). Kurunegala District: Kurunegala, *Thwaites C.P. 2878* ex p. (PDA); Kurunegala Rock, *Alston 699* (PDA); Wariyapola, *Trimen* Aug. 1883 (PDA); Siyambalatenna, *Alston 596* (PDA). Ratnapura District: *ca.* 13 miles N.E. of Deniyaya at Mile 64 on Rd. A 17, 1050 m alt., *Davidse 7899* (MO, NY, PDA, US). Galle District: Galle, *Alston 289* (PDA). Ruhuna National Park: Rugamtota, *Cooray* 16 Nov. 1969 (NY, US).

While in Ceylon I was able to investigate the variation ranges of leaf width and the intensity of the umbels in this very common species. My conclusion is that var. *roxburghianus* should not be retained. It was claimed to differ from the typical phase in the relatively broader leaves and larger umbels.

50. **Mariscus clarkei** (T. Cook) T. Koyama, Journ. Jap. Bot. **51** (10): 313, 1976. ——— **Fig.** 9

Cyperus clarkei T. Cook, Fl. Presid. Bombay **2**: 873, 1908; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 540, *f. 58*, 1936. ——— [*Mariscus pictus* Nees in Wight, Contrib. Bot. India 90, 1834, in part excluding type.] ——— [*Mariscus bulbosus* C. B. Clarke, Fl. Brit. India **6**: 620, 1893; C. E. C. Fischer in Gamble, Fl. Madras **9**: 1644, 1931. Not. of Steudel, 1855.] ——— [*Kyllinga bulbosa* Vahl, Enum. Pl. **2**: 376, 1806, invalid name mentioned in note; Römer & Schultes, Syst. Veg. **2**: 247, 1817, in note.]

Monaragala District *ca.* 11 miles W of Tanamalwila, 125 m alt., *Davidse & Sumithraarachchi 8812* (MO, NY, PDA, US). Hambantota District: Ruhuna National Park, Kohombagaswala, *Cooray* 23 Nov. 1969 (NY, PDA, US).

Distribution. Confined to southern India and Ceylon.

This species, newly found in Ceylon, rarely grows on wet shallow soil over rock outcrops. It is well demarcated by the peculiar bulb-shaped base, which emits a few slender stolons. The umbel of this species resembles that of *M. cyperinus*, and hence it is never confused with *M. dubius*, another bulbose *Mariscus* in Ceylon.

51. **Mariscus dubius** (Rottboell) Kükenthal ex Fischer in Gamble, Fl. Madras **9**: 1644, 1931.

Cyperus dubius Rottboell, Descr. Icon. Rar. Pl. 20, *t. 4 f. 5*, 1773; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 563, 1936; Kern, Fl. Males. I, **7** (3): 643, 1974. ——— *Cyperus kyllingaeoides* Vahl, Enum. Pl. **2**: 312, 1806. ——— *Mariscus dregeanus* Kunth, Enum. Pl. **2**: 120, 1837; C. B. Clarke, Fl. Brit. India **6**: 620, 1893, & Illustr. Cyper. *t. 21 f. 1-6*, 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 39, 1900.

Anuradhapura District: Ritigala Natural Reserve, on summit rock, 2500 ft. alt., *Jayasuria 905* (PDA). Polonnaruwa District: Lankatilaka, *Silva 182* (PDA). Kurunegala District: Kurunegala, *Thwaites C.P. 2942* (K, PDA) & *C.P. 855* (K, PDA). Kandy District: Aladeniya, *Amaratunga 642* (PDA); between Balane and Alagalla, 440 m alt. *Comanor 1194* (NY, US). Badulla District: Rawanaella Waterfall, ca. 2 miles SE of Ella, 750 m alt., *Davidse et al. 8866* (MO, NY, PDA, US); Lunugala, *Trimen* Jan. 1888 (PDA). Monaragala District: *ca.* 11 miles W of Tanamalwila, 125 m alt., *Davidse et al. 8802* (MO, NY, US, PDA). Galle District: Galle, *Gardner C.P. 855* (K, PDA). Ruhuna National Park: Bambowa, *Cooray* 17 Nov. 1969 (NY, US); Rugamtota, *Cooray* 16 Nov. 1969 (NY, US).

Distribution. Tropical Africa through India and Indo-China eastwards to Malesia.

52. **Mariscus pedunculatus** (R. Brown) T. Koyama, *comb. nov.*

Remirea maritima Aublet, Hist. Pl. Guian. Franc. **1**: 45, *t. 16,* 1775. Not *Mariscus maritimus* Miquel, 1860, nor of C. B. Clarke, 1896. ——— *Remirea pedunculata* R. Brown, Prodr. Fl. Nov. Holl. 236, 1810. ——— *Cyperus pedunculatus* (R. Brown) Kern, Act. Bot. Neerl. **7**: 798, 1958.

Jaffna District: Jaffna, *Thwaites C.P. 3227* (K, PDA). Colombo District: Colombo, *Ferguson C.P. 3227* (PDA); Mt. Lavinia, *Trimen* Oct. 1881. (PDA).

Distribution. Southern Asia, Malesia and northern Australia; also in tropical America from eastern Venezuela through the Guianas south to Brazilian Paraná Sand dunes and sandy shores of sea coast.

The cyperoid morphology exhibited by this species was fully discussed by Kern (op. cit.), with whom I concur. When *Cyperus* sensu lato is divided into a few genera, this species properly belongs to *Mariscus* because of its continuous rhachilla jointed at its base.

KYLLINGA Rottb.

1. Inflorescence open, umbelliform with elongated rays .... **53** *K. hyalina*

1. Inflorescences congested in a head

    2. Glumes not winged

        3. Rhizome short; culms tufted

            4. Central spike cylindrical or oblong, 8–15 mm long, ca. 5 mm wide; spikelets broadly ovate, 2 mm long; culms slightly or hardly enlarged at base .... **54** *K. odorata* ssp. *cylindrica*

            4. Central spike globose or ovoidal, 5–6 mm long, 3–4 mm across; spikelets oblong-elliptical, 1.7–2 mm long; culms bulbose-thickened at base .... **55** *K. triceps*

        3. Rhizome horizontally creeping or stoloniferous; culms distantly or closely arranged in one row along rhizome

            5. Culms 30–50 cm tall, close together

                6. Leafy bracts 2 or 3 .... **56** *K. melanosperma*

                6. Leafy bracts 6 to 8 .... **57** *K. polyphylla*

            5. Culms as a rule 7–30 cm tall, more or less spaced ....
            .... **58** *K. brevifolia*

    2. Glumes winged .... **59** *K. nemoralis*

Fig. 10. *Kyllinga hyalina* (Vahl) T. Koyama. *A*, habit. *B*, portion of rhachis with bracteoles and prophylls remaining after spikelets falling off. *C*, spikelet. *D*, prophyll. *E*, lateral view of two glumes. *F*, lateral view of achene. Scales = 1 mm.

53. **Kyllinga hyalina** (Vahl) T. Koyama, Journ. Jap. Bot. **51** (10): 313, 1976. ——— **Fig. 10**

Cyperus hyalinus Vahl, Enum. Pl. **2**: 329, 1806; Trimen & Hook. f. Handb. Fl. Ceylon **5**: 19, 1900; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 498, 1936; Kern, Fl. Males. I, **7** (3): 655, *t. 68*, 1974. ——— *"Cyperus pumilus* L.": sensu Nees in Wight, Contrib. Bot. Ind. 74, 1834. ——— *"Pycreus pumilus"* C. B. Clarke, Fl. Brit. Ind. **6**: 591, 1893, concerning description. ——— *Pycreus hyalinus* (Vahl) Domin, Bibl. Bot. Heft **85**: 417, 1915, in obs. ——— *Queenslandiella mira* Domin, Bibl. Bot. Heft **85**: 416, *t. 11 f. 7-13*, 1915. ——— *Mariscopsis suaveolens* Chermezon, Bull. Mus. Paris **25**: 60, 1919. ——— *Mariscopsis hyalinus* (Vahl) Ballard, Kew Bull. **1932**: 457, 1932. ——— *Queenslandiella hyalina* (Vahl) Ballard in Hook., Icon. Pl. **33**: *t. 3208*, 1933.

Anuradhapura District: Anuradhapura, *Trimen* 18 Dec. 1881 (PDA). Kurunegala District: Kurunegala, *Trimen C.P. 3787* (K, PDA); Kuliyapitiya, *Simpson 9159* (PDA). Ruhuna National Park; near turn off to Andunoruwa Wewa, *Cooray* 10 Dec. 1969 (NY, PDA, US); Ecology Project Block I, Plot R 13, *Cooray* 7 Dec. 1969 (US).

Distribution. Tropical East Africa, Mascarene Is., India, Indo-China, Malesia and northern Australia. Sporadically occurring in dry grasslands.

When we split the genus *Cyperus* of broad meaning into several genera of smaller size, the systematic attribution of *Cyperus hyalinus* deserves special mention. Morphologically this species doubtlessly falls within the generic criterion of *Kyllinga,* from which it slightly deviates in having open inflorescences and in the spikelets of which nearly all the glumes are fruit-bearing. However, in the genus *Kyllinga,* umbel rays really develop as seen in *K. transitoria* for instance, and further where in all the cyperoid genera both open and head-like inflorescences occur without any clear border, thus showing that these conditions of inflorescences do not warrant generic segregation. Similarly the number of fruit-bearing glumes in a spikelets also does not serve as a distinguishing character between genera. In *Mariscus,* the genus most closely related to *Kyllinga,* both multi- and few-flowered spikelets coexist (cfr. *M. cyperinus* vs. *M. javanicus,* for example). It is therefore permissible to include *Cyperus hyalinus* in *Kyllinga* in spite of the multi-flowered spikelets. In reality *Cyperus hyalinus* strikingly resembles *Kyllinga* ssp. not only in its bilaterally flattened oblong-elliptic achenes but also in its thinly membranous glumes with several prominent veins on both sides of the midrib.

54. **Kyllinga odorata** Vahl, Enum. Pl. 2: 382, 1906.

This species, occurring in tropical America and Africa, is represented in Ceylon by:

subsp. **cylindrica** (Nees ex Wight) T. Koyama, *comb. nov.*

Kyllinga cylindrica Nees ex Wight, Contrib. Bot. Ind. 91, 1834; C. B. Clarke, Fl. Brit. Ind. **6**: 588, 1893, incl. var. *subtriceps* Nees; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 44, 1900. ——— *Kyllinga odorata* Vahl var. *cylindrica* (Nees) Kükenthal ex Merrill, Journ. Str. Branch Roy. As. Soc. **76**: 80, 1917. ——— *Cyperus sesquiflorus* (Torrey) Mattfeld & Kükenthal var. *cylindricus* (Nees) Kükenthal, Pflanzenr. **4** (20), 101 Heft: 593, 1936. ——— *Cyperus sesquiflorus* Mattfeld & Kükenthal subsp. *cylindricus* (Nees) T. Koyama, Bot. Mag. Tokyo **83**: 187, 1970. ——— *Cyperus sesquiflorus* Mattfeld & Kükenthal var. *subtriceps* (Nees) T. Koyama, Quart. Journ. Taiwan Mus. **14**: 191, 1961; Kern, Fl. Males. I, **7** (3): 659, 1974.

Kandy District: Pusselawa, *Alston* 19 Sept. 1926 (PDA). Badulla District: Haldummulla, *Thwaites C.P. 3754* (K, PDA). Nuwara Eliya District: Ohiya, *Mueller-Dombois* 18 May 1968 (PDA, US); Hakgala, *Simpson 9041* (PDA);

Ramboda, along N. Eliya Rd., 1180 m alt., *T. Koyama & Herat 13619* (NY, PDA, US). Hambantota District: Ruhuna National Park, *Cooray* 30 November 1967 (PDA, US).

Distribution. Tropical Africa, tropical and subtropical Asia.

The morphological differences between subsp. *cylindrica* and the typical phase were discussed in my previous paper (Koyama, op. cit. 1970).

55. **Kyllinga triceps** Rottboell, Descr. Icon. 14, *t. 4 f. 6,* 1773; C. B. Clarke, Fl. Brit. Ind. **6**: 587, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 45, 1900.

[*Schaenoides triceps* Rottboell, Descr. Pl. Rar. Progr. 15, 1772, invalid name.] ——— *Cyperus triceps* (Rottb.) Endlicher, Cat. Hort. Acad. Vindb. **1**: 94, 1842; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 578, 1936; Kern, Fl. Males. I, **7** (3): 659, 1974.

Mannar District: Aruvi Aru, Mile 125 on Rd. A 14, *T. Koyama et al. 13932* (NY, PDA, US). Polonnaruwa District: Polonnaruwa Sacred Area, Sect. 3A, 61 m alt., *Ripley 334* (US); Polonnaruwa-Trincomalee Rd., *Clayton 5136* (K, PDA). Matale District: 33/7 Midlands, *Tilvengadum et al. 12* (US). Puttalam District: Anamaduwa, *Trimen* Aug. 1883 (PDA); Puttalam, *Brodie C.P. 3234* in part (PDA). Colombo District: Colombo, *Thwaites C.P. 3234* (K, PDA). Monaragala District: *ca.* 11 miles W of Tanamalwila, 125 m alt., *Davidse et al. 8810* (MO, NY, PDA). Ruhuna National Park: Komawa Wewa, *Cooray* 16 Nov. 1969 (PDA, US); Gonalabbe, *Cooray* 24 Nov. 1969 (NY, PDA); Yala, Andunoruwa Wewa, *Comanor 673* (NY, US).

Distribution. From tropical Africa through India and Indo-China northeastwards to southern China, and eastwards to Malesia and northern Australia.

56. **Kyllinga melanosperma** Nees in Wight, Contrib. Bot. India 91, 1834; C. B. Clarke, Fl. Brit. India **6**: 588, 1893; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 45, 1900.

Cyperus melanospermus (Nees) Suringar, Het. Gesl. Cyperus Mal. Archip. 50, *t. 2 f. 8,* 1898; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 583, 1936; Kern, Fl. Males. I, **7** (3): 655, 1974.

Kandy District: Peradeniya, Lower Hantana Rd., near the waterfall, 535 m alt., *Comanor 692* (NY, US); between Pusselawa and Ramboda, *Comanor 950* (PDA); between Laxapana and Maskeliya Rd., *Kostermanns 24079* (PDA); Ambagamuwa, *Amaratunga 2014* (PDA), between Udahentenna and Nawalapitiya, *Amaratunga 909* (PDA); Aladeniya, *Amaratunga 1643* (PDA). Nuwara Eliya District: Hakgala, *Wheeler 12371* (PDA); Nuwara Eliya, *Thwaites C.P. 818* (K, PDA); Horton Plains, forest opposite to the Horton Plains Farm, along Pattipola Rd., 7200 ft. alt., *T. Koyama 13506* (NY, PDA, US); base of Hakgala Mtn. 1870 m alt., *Davidse et al. 7981* (MO, NY, PDA, US). Badulla District: *ca.* 3 miles W of Koslanda, along Rd. A 4, *ca.* 900 m alt., *T. Koyama et al. 14033* (NY, PDA, US). Colombo District: Wattala, *Comanor 1153* (PDA, US); Danowita; *Amaratunga 193* (PDA); Kimbulapitiya, *Amaratunga 2157* (PDA). Ratnapura District: 11 miles E of Diniyaya, near Mile 62 on Rd. A 17, 750 m alt., *Davidse 7875* (MO, NY, PDA, US). Galle District: Corbett's Gap. 4500 ft. alt., *Ballard 1052* (K, NY).

Distribution. Tropical and subtropical Africa, southern Asia, Fiji and Malanesia. In Ceylon common on the grassy beds of montane forests.

This species, well characterized by its relatively thick leafless culms and large heads, can be easily located in the field because of its strong odor of essential oil, which is contained in the thick rhizome.

57. **Kyllinga polyphylla** Willdenow ex Kunth, Enum. Pl. **2**: 134, 1937.

Kyllinga aromatica Ridley, Trans. Linn. Soc. II, Bot. **2**: 146, 1884. ——— *Cyperus aromaticus* (Ridley) Mattfeld & Kükenthal, Pflanzenr. **4** (20), 101 Heft: 581, 1936; T. Koyama, Bot. Mag. Tokyo **83**: 186, 1970; Kern, Fl. Males. I, **7** (3): 656, 1974.

Nuwara Eliya District: between Pussellawa and Ramboda, at Mile 28/10 along Kandy-N. Eliya Rd., 950 m alt., *Comanor 328* (NY, PDA, US).

Distribution. E. Africa. Also introduced to Singapore, Ceylon, Solomon Islands, Samoa and Fiji.

This African species can be separated from the closely allied indigenous species, *K. melanosperma,* by its head subtended by 6 to 8 leafy bracts in contrast to 2 or 3 in the latter. In Ceylon it is thus far known only by the collection cited above, and is apparently of rather recent introduction.

58. **Kyllinga brevifolia** Rottboell, Descr. Icon. Rar. Nov. Pl. 13, *t. 4 f. 3,* 1773; C. B. Clarke, Fl. Brit. India **6**: 588, 1893, & Illustr. Cyp. *t. 1 f. 1-4,* 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 45, 1900.

[*Schaenoides brevifolius* Rottb., Descr. Pl. Rar. Progr. 15, 1772, invalid name.] ——— *Cyperus brevifolius* (Rottb.) Hasskarl, Cat. Hort. Bogor. 24, 1884; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 600, 1936; Kern, Fl. Males. I, **7** (3): 656, f. 70, 1974.

Wilpattu National Park: Kali Villu, *Wirawan et al. 990* (US). Mannar District: Aruvi Aru, Mile 125 on Rd. A 4, *T. Koyama et al. 13926* (NY, PDA, US). Kandy District: Peradeniya, Upper Hantana Rd., 550 m alt., *Comanor 315* (NY, US); Ambewela, *Mueller-Dombois* 12 Jan. 1968 (PDA, US). Nuwara Eliya District: Kande Ela Reservoir, *Mueller-Dombois* 18 May 1968 (PDA). Colombo District: Dompe, *Amaratunga 2182* (PDA); Ranmuthugal, *Amaratunga 2221* (PDA). Galle District: Galle, *Trimen C.P. 3755* (K, PDA).

Distribution. Pantropic; in Asia extending northwards into the warm regions of continental China and the temperate region of Japan.

This cosmopolitan weedy sedge is rather poorly documented in Ceylon. Since it frequently grows in and around rice fields, it is quite possible that this sedge extended its range with the introduction of rice as assumed for *Cyperus iria* and *Fimbristylis miliacea.*

59. **Kyllinga nemoralis** (J. R. & G. Forster) Dandy ex Hutchinson & Dalziel, Fl. W. Trop. Africa **2**: 486, in Key, & 487, 1936.

[*Kyllinga monocephala* Rottboell, Descr. Icon. Rar. Nov. Pl. 13, *t. 4 f. 4,* 1773, invalid name; C. B. Clarke, Fl. Brit. India **6**: 588, 1893 & Illustr. Cyper. *t. 2 f. 1-2,* 1909; Trimen & Hook. f., Handb. Fl. Ceylon **5**: 44, 1900.] ——— *Cyperus kyllingia* Endlicher, Cat. Hort. Acad. Vindb. **1**: 94, 1842; Kükenthal, Pflanzenr. **4** (20), 101 Heft: 606, *f. 64,* 1936; Kern, Fl. Males. I, **7** (3): 659, 1974. ——— *Thryocephalon nemoralis* J. R. & G. Forster, Char. Gen. Pl. 130, 1776.

Trincomalee District: Mutur, *Wheeler 12425* (PDA). Kandy District: Roseneath, 2101 ft. alt., *Ballard 1014* (K, NY). Monaragala District: *ca.* 3 miles W of Wellawaya at Mile 135/10 on Rd. A 4, 990 ft. alt. *Davidse 7728 & 7732* (MO, NY, PDA, US). Ruhuna National Park: Rugantota, Block I, *Cooray* 16 Nov. 1969 (NY, US); Ecology Project Block I, Rugantota on Minik Ganga, *Fosberg et al. 50191* (NY, US).

Distribution. Pantropic, relatively scarce in tropical America.

It is unfortunate that to this common species, which has long been known as *Kyllinga monocephala,* must be assigned an unfamiliar epithet as its correct name. Rottboell's *Kyllinga monocephala* is invalid as the name was published with an earlier legitimate name, *Schoenus coloratus* L., cited in the synonymy.

Literature Cited outside Taxonomic Enumerations

Kern, J. H. 1974. Cyperaceae. Flora Malesiana Ser. I, **7** (3): 435–753.

Koyama, T. 1970. Beiträge zur Cyperaceenflora von Ceylon. Bot. Mag. Tokyo **83**: 183-192.

——————— 1974. Additional notes on Ceylonese Cyperaceae. Bull. National Sci. Mus. Tokyo **17**: 65-73.

Kükenthal, G. 1935-36. Cyperaceae-Scirpoideae-Cypereae. Pflanzenr. **4** (20), **101** Heft: 1–671.

Trimen, H. & J. D. Hooker. 1900. A Handbook to the Flora of Ceylon **5**: 1-477.

The Limestone Hill Flora of Malaya I

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CONTENTS

Abstract

Limestone habitats, chiefly karst towers, in the Malayan Peninsula, support a rich flora of about 1216 species of vascular plants, in 582 genera and 124 families. Phanerogam families total 119, representing 61.6% of the total number of phanerogam families recorded for the whole Malayan flora; only 72 families are not represented on limestone, and these are mostly aquatics or small rare groups. Specific endemism among the limestone plants is 21.4% (261 species), and of these 10.7% (130 species) are found only on limestone. There are 335 species "characteristic" of the limestone flora, and 254 of these (20.8%) are restricted to limestone.

The limestone vegetation is described and classified into "types" and secondary vegetation and succession is discussed. Pioneer species on limestone include those found on other disturbed terrestrial habitats in Malaya. Some plants found on limestone are found elsewhere in Malaya only at significantly higher elevations. A discussion of the geological origin and distribution of the Malayan limestone areas is also included.

Preface and Acknowledgements

This publication is based on the dissertation accepted for the Master of Science Degree in 1973 by the School of Biological Sciences, University of Malaya. I am grateful to Professor van Steenis, external examiner, for his critical comments and helpful suggestions.

My work was supervised by Dr. B. C. Stone who introduced me to this topic, provided an unfailing source of guidance, and who also permitted me free access to his most remarkable collection of botanical literature which has been an inspiring and invaluable source of reference. I am also grateful for his encouragement to publish this work.

The Department of Botany, University of Singapore allowed me the use of their herbarium and Dr. H. Keng helped with the identification of several Labiatae. He also generously provided me with the records of the collection made by the UNESCO 1962 limestone expedition to Ulu Kelantan. These consisted of a map, several note books and a set of duplicate labels to the collection.

The Director of the Botanic Gardens, Singapore, gave me permission to work and the staff helped me in the herbarium on several occasions.

Dr. T. C. Whitmore and subsequently Dr. Francis Ng allowed me to use freely the facilities of the herbarium at the Forest Research Institute, Kepong, and manuscripts of their 'Tree Flora of Malaya', vol. 2 then in press. Dr. Whitmore also helped with the identification of some Garcinias, Euphorbiaceae and Palms; Dr. Ng with some Ebenaceae and other members of the staff with some general collections.

Dr. K. U. Kramer of the State University, Utrecht, Netherlands, identified several fern specimens and Dr. T. Shimizu of Shinshu University, Japan, provided literature and helped with the identification of a specimen of *Impatiens*.

With Dr. P. R. Wycherley, formerly of the Rubber Research Institute, Kuala Lumpur, I had interesting discussions and he also introduced me to the Johore limestone.

Mr. W. Swinson, Project Manager for the South East Johore Project, then engaged in a Master Plan Study of South East and Central Johore for the Government of Malaysia and State Government of Johore and his staff provided maps, transport, guides and equipment for two trips into the Gunong Sumalayang limestone outcrops in Johore. Mr. Swinson also provided unpublished data on the locality.

Dato Haji Wan Hassan bin Abdul Halim, the State Forest Officer of Johore gave permission to enter and botanize in the Johore limestone area.

Incik Mahmud bin Sidek and Incik Badaruddin, field investigator and herbarium assistant respectively, assisted in several excursions. Friends, particularly J. Boey, provided help and interesting company on numerous trips to the limestone.

To all these helpful persons I express my most grateful thanks.

I must also state my appreciation for the comments of Dr Chang Kiaw Lan, editor.

Most of this work was carried out during the tenure of a tutorship in the School of Biological Sciences, Universiti Malaya.

SECTION 1 — General

1. INTRODUCTION

Background to the flora

The limestone landscape in Malaya is very distinctive. Typically the hills are tower-like, rising from the surrounding scenery, with sheer rock walls and often jagged summits. These 'tower karst' formations occur as isolated crags or are grouped together into small massifs — all products of erosion of calcareous rock. Erosion too is responsible for the presence of caves that often characterize limestone hills. These caves have, since prehistoric times, often been used as human dwellings, and as much as the vegetation on the hills provide clues to the history and evolution of the Malayan flora, provide evidence for an insight into prehistoric Malayan culture.

Most of the past work on the Malayan limestone concerned the geology, origin and age of the rock, e.g. Scrivenor (1931), Paton (1961, 1964), Gobbett (1965) and Hutchison (1963, 1968). Other investigators have concerned themselves with cave archaeology, e.g. Evans (1920), Tweedie (1940) and Peacock (1965), or cave ecology and fauna, e.g. Bullock (1963, 1965), Dunn (1965), McClure (1965) and Tweedie (1947).

The only separate work on the flora is that of Henderson (1939). This contains an introduction giving the collecting localities, with notes on the vegetation and the characteristics of the flora. The localities are introduced state by state; the chief hills are named and the major collectors mentioned. There is however, no map of the distribution of the hills mentioned. The vegetation is described; there is a division of the hills into two main groups, the 'wet' and 'dry' hills. The frequency of the occurrence of the plant families (restricted to the spermatophytes) is briefly summarized.

A total of about 745 species is recorded from the limestone by Henderson. The species are presented in a check-list with short distributional notes; the arrangement of the families follows Ridley (1922-25), while the genera and species are arranged in alphabetical order. Of the 745 species recorded about 195 (26%) in the Peninsula are known only from limestone. The species endemic and confined to the limestone number about 130.

Apart from this study, species distribution on limestone is sometimes mentioned in floristic or monographic works on the local flora. Thus this well known habitat is, botanically, relatively unworked.

The history of botanical exploration on the Malayan limestone hills began in August 1880 when Kunstler, collector for Sir George King, made a collecting trip to the Gopeng limestone in Perak (the exact locality is unknown). Other early collectors (before 1900) include Curtis, Fox, Kelsall, Ridley and Wooldridge. Up to the present day more than 60 collectors have left their mark on this history. Their efforts have accumulated about 4,500 numbers (an estimate based on my having seen about 4000 numbers and assuming that I have not seen about 10% of the total); of this the writer contributed 1550 numbers.

The total area of limestone in Malaya, considering the average height to be 243.8 m (800 ft), is about 260 sq. km. (an estimate based on Scrivenor, in Burkill, 1935). Therefore per unit area the limestone may seem to have been very intensively botanised, with about 1962 numbers per 100 sq. km. (compared with the average of 175 numbers per sq. km. for the whole of Malaya, Steenis-Kruseman, 1973). These figures are, however, deceptive and misleading when the richness of the limestone flora is taken into account. The total number of collections from the Malay Peninsula is about 232,000 (a rough estimate based on Steenis-Kruseman, 1973) and the total species present in Malaya is estimated to be between 8000–8500 (Keng, 1970). This total number of species is an estimation only and is more than the number of species presently known. Thus this shows that on the average, each species is represented by 26–29 numbers. On the other hand, 1216 species are recorded from the limestone (present study) which are represented by about 4500 numbers, thus giving an average of about 4 numbers per species. Even if only the characteristic species (with affinities for the limestone habitat) were considered (they number 335 and the total numbers collected would also drop far below 4500) and the total numbers collected be retained at 4500, the average number of specimens per species will be 13, which is still low.

Besides low total numbers collected with respect to the extremely rich flora, many of the limestone species have a very local distribution which intensifies the problem of insufficient collection. Though most of the limestone localities have been visited by botanists, the total number of hills actually climbed and collected on is only about 50, and the number of islands (in Langkawi) visited is about 25 (the writer has visited 25 hills and 12 islands, some repeatedly). There are no estimates of the total number of limestone hills in Malaya, but they probably number well over 200, and Langkawi consists of 99 islands (though not all are limestone, a large percentage are). Thus we have a situation where many hills, islands and localities have been repeatedly visited while others have not been botanised at all. The "popular" localities include Bukit Takun, Gunong Rapat, Gua Musang, Pulau Dayang Bunting (around the lake), Pulau Jerkom and Pulau Timun. However, this is not to say that these relatively frequently visited spots are sufficiently botanised. For instance, recently I discovered a clump of *Oncosperma horridum* on the summit of Gua Batu (which rates high on the list of popular localities), a species which has not been recorded on the limestone before. Considering that Gua Batu is less than 2.59 sq. km (1 sq. mile), in area, this clearly shows that the many rugged faces of a limestone hill can conceal even the most conspicuous plant.

Therefore in relation to its rich flora, extremely varied habitat and the fact of uneven local exploration, the limestone vegetation is probably the least botanised, and hence botanically known, of all the vegetation types in Malaya.

The collectors who have contributed to our knowledge of the limestone flora are listed below with a brief mention of collection dates and localities.

Collectors

Allen, B.E.G.M. Dec. 15th. 1950; Gunong Keriang (Kedah), a specimen of *Chirita viola* Ridl. 1958–1960; widely in Perak, visited Gunong Idong, Gunong Kanthan, Rotan Segar. Almost 100 numbers.

Allen, E.F. May 1946; collected on 'Kinta limestone'. April 1955–Jan. 1957; collected on several occasions from Gua Batu and Bukit Takun in Selangor.

Alphonso, A.G. & A. Samsuri. Nov.–Dec. 1960; several numbers from Langkawi (Pulau Bumbon Besar and Bumbon Kechil).

Batten Pooll, A.H. A poorly labelled *Dendrocalamus elegans* (Ridl.) Holtt. from the Langkawi limestone.

Best, G.A. Oct. 29th–Nov. 3rd, 1929; miscellaneous, about 80 numbers from Gunong Baling, Kedah.

Boey, H.Y. July 1970 — Sept 1971; collected from Bukit Takun on four occasions and once from Bukit Anak Takun, Selangor. August 1971; collected from Gua Musang, Gua Batu Boh, Batu Neng and Batu Tapah (all in Kelantan) and Gua Layang, Pahang. November 1971; visited Langkawi and collected from a number of limestone islands. About 350 numbers in all.

Burkill, I.H. 1916–1920; collected from Gua Batu, Selangor and around Ipoh, Perak. Sometimes with Haniff.

Burtt, B.L. & Woods, P.J.B.; Langkawi, at Sungei Kisap and Pulau Dayang Bunting; Perlis at Bukit Chupeng and Bukit Bintang; Perak, around Ipoh. About 146 numbers in all.

Carr, C.E. 1928–1930; visited Kota Glanggi, Gunong Senyum, Gua Tipus and Tembeling in Pahang. Collected mainly orchids; some ferns also.

Chan, Y.C. July 1970; collected from around Lenggong, Perak. Several assorted numbers.

Chew, W.L. April–May 1957; collected on Bukit Hantu, Bukit Kalong, Gunong Baling and around Dayang Bunting, Langkawi; all in Kedah. In the same period also visited Bukit Manek and Kaki Bukit in Perlis.

Cockburn, P.F. June 10th 1968; some specimens from Batu Biwa in Trengganu.

Corner, E.J.H. Nov. 16th–25th, 1929 (with Henderson); collected on Bukit Lagi, Perlis. 1936–1937; visited Ipoh and Bukit Takun. Nov. 13th-22nd 1941 (sometimes with Nauen); collected from all over Langkawi, resulting in some 200 numbers. 25th Nov. 1941 (with Nauen); collected on Gunong Baling, Kedah.

Curtis, C. 1888–1902; visited Langkawi (Kedah), Gua Batu in Selangor, Kinta district, around Ipoh and Sungei Siput in Perak. Most of the specimens are very poorly labelled.

Durant, C.L. Oct. 30th 1940; a specimen of *Maxburretia rupicola* (Ridl.) Fur. from Bukit Takun (Selangor).

Dransfield, J. July 31st 1968; several orchids from Bukit Anak Takun (Selangor),

Enoch, I. Sept. 25th 1954; a specimen of *Impatiens mirabilis* Hk.f. from Pahang.

Evans, G.B. Early 1966; Ipoh Temple limestone (Perak) and Bukit Takun (Selangor); several ferns.

Everett, B. July 1970; collected from around Lenggong, Perak. Eighteen numbers.

Fox, W. 1899-1904; several plants from Langkawi (Kedah) and around Ipoh (Perak).

Furtado, C.X. June 4th 1937; several palms and two aroids from Gunong Baling, Kedah.

Haniff, Mohamed. 1900–1921; collected occasionally from limestone, visited Bukit Wang, Gunong Keriang and Langkawi (Kedah), and Gunong Pondok (Perak). After 1918 usually with Nur. *See also* Burkill.

Hashim, Ja'afar. Collected a *Wikstroemia indica* (L.) C.A. Mey from Langkawi.

Henderson, M.R. 1923–1935; visited most of the limestone localities. Langkawi, usually on both sides of Selat Panchor (straits), and around Pulau Dayang Bunting. Gua Lambok, Gua Musang, Gua Panjang and Gua Teja (Kelantan). Bukit Cheras, Bukit Chintamani, Bukit Serdam, Gua Tipus, Gunong Senyum and Kota Glanggi (Pahang). Gua Lanno, Gunong Pondok, Ipoh, Lenggong and Pulai (Perak). Besih Hangat, Bukit Chupeng, Bukit Lagi, Bukit Wang Tangga and Tebing Tinggi (Perlis). More than 700 numbers,

Holttum, R.E. Oct. 3rd 1922; Gua Batu, Selangor, several ferns. Aug. 22nd-26th 1925; Langkawi, around Pulau Dayang Bunting and Pulau Timun. About 25 numbers.

Johnson, A. Nov. 17th 1968; several ferns from Gua Batu, Selangor.

Kadim, Tassim. Aug. 13th 1959 (with Allen, B.E.G.M.); several numbers from Gunong Tempurong, Perak.

Kassim, Rajab. Aug. 17th 1962; several numbers from Gua Batu, Selangor.

Kelsall, H. Jan. 1891; several plants from Gua Batu, Selangor; all poorly labelled.

Keng, H. Sept. 25th 1954; at Kuala Trengganu, several ferns. Mar. 28th 1962 (with Mrs. Keng); a specimen of *Monophyllaea horsfieldii* R. Br. Nov. 3rd–7th. 1968; Langkawi islands (sometimes with others); some assorted specimens.

Kerr, A.F.G. June 20th 1932; Langkawi, around Kuah; several numbers.

Kiah, Hj.M.S. April 11th-May 9th 1938; collected on Gunong Baling, Kedah and Kaki Bukit, Perlis. More than 150 numbers.

King, Sir G. *See under* Kunstler.

Kunstler, H.H. (collector for Sir G. King, as King's collector) 1880–1885; collected around Gopeng and Larut, also visited Gunong Pondok (all in Perak). Almost 100 numbers.

Loh, H.S. July 1970; Gua Peningat, Pahang. Recorded 101 numbers. This is the first known occasion that this outcrop (at 713 m the tallest in Malaya) has been climbed. February 1972; visited Gua Musang, Kelantan. Sixteen numbers.

Mahmud, S. 1970–1971; Bukit Anak Takun (Selangor), and Ipoh (Perak). Several numbers *See also* Samsuri.

Mat Sani, W. Jan. 1939; a specimen of *Cymbogon calcicola* Hubb. from Gunong Baling, Kedah.

Merton, L.F.H. Dec. 22nd 1960; Gua Batu, Selangor; several numbers.

Mills, G.R. April 16th 1925 (with Henderson); Gunong Lanno, Perak; several specimens.

Nauen, J.C. Nov. 13th–17th 1941; Gunong Baling and Langkawi, both in Kedah. About 20 numbers. *See also* Corner.

Ng, F.S.P. Oct. 1966–Feb. 1968; Gunong Mesah, Gunong Rapat, Gunong Tempurong and other hills around Ipoh (all in Perak). Gua Batu and Bukit Takun in Selangor and Gua Musang in Kelantan. More than 150 numbers.

Nur, Mohamed. 1931–1937; Bukit Sagu, Pahang and Bukit Takun and Gua Batu, Selangor. *See also* Haniff. About 160 numbers.

Ogata, K. Feb. 14th–15th, 1968; Gunong Gajah and Gunong Tempurong in Perak. Some assorted specimens.

Phang, C.I. Sept. 15th 1960; several ferns from Bukit Anak Takun, Selangor.

Poore, M.E.D. Sept. 12th 1960 & July 16th 1961; visited Gua Batu, Selangor. Several numbers.

Reid, J. Jan. 29th 1950; three numbers from Bukit Takun, Selangor.

Ridley, H.N. 1896–1897; visited Kuala Dipang (Perak) and Gua Batu, Selangor 1898–1920; visited Gua Batu about five times, also Gunong Keriang, Kedah and Bukit Lagi, Perlis. About 150 numbers.

Samat, A. 1961–1969; visited Langkawi (Kedah), Bukit Anak Takun and Bukit Takun (Selangor). Mainly ferns; about 15 numbers.

Samsuri, A. Mar. 8th–14th, 1971 (with Mahmud); collected in Perak, around Gopeng, on Gua Putri, Gunong Pondok, Gunong Rapat, around Ipoh, and in Tambun district. About 120 numbers.

Shimizu, T. Oct.–Nov. 1967 (with Stone); visited Gua Musang (Kelantan) and Bukit Takun (Selangor). Some ferns.

Sinclair, J. 1958–1962; visited hills around Ipoh (Perak) and Gua Batu (Selangor). About 30 numbers.

Singh, Hardial. Jan. 23rd 1966; visited Gua Batu (Selangor). Several numbers.

Smith, G. One *Chirita caliginosa* Cl. from Perak Cave Temple.

Smith, J.W. July 19th 1956; one *Vitex siamica* Will. from Gunong Baling, Kedah.

Soepadmo, E. Sept. 1968; one *Carallia brachiata* (Lour.) Merr. from Ipoh, Perak.

Spare, G.H. Oct. 1st 1939; Gunong Pondok, Perak. Several numbers.

Start, A. Jan. 23rd 1972; one *Mucuna biplicata* Teysm. et Binn. from Bukit Anak Takun, Selangor.

Stone, B.C. 1965–1972; visited Langkawi (many of the islands), Kedah, Gua Musang (Kelantan), Gunong Pulai (Perak), Bukit Anak Takun, Bukit Takun and Gua Batu (Selangor). Chintamani (Pahang). About 450 numbers.

Students (University of Malaya 1967) May 1967; some numbers from Langkawi (Kedah).

Symington, C.F. 1934–1938; visited Langkawi (Kedah) and Bukit Takun. About a dozen numbers.

Teruya, Z. Jan. 20th 1929; one *Monophyllaea horsfieldii* R. Br. from Gua Batu, Selangor.

Tomlinson, P.B. Sept. 1955; one *Monophyllaea hirticalyx* pr. from Ipoh Perak.

Turnau, E.A. Aug. 5th 1962; two numbers from Langkawi, Kedah.

UNESCO 1962 July 27th-Aug. 13th, 1962; visited the Kelantan limestone around Gua Musang and Bertam, collected on Batu Bayan, Batu Hayan, Batu Ner, Batu Pinta, Gua Batu Boh, Gua Musang, Gua Serai, Gua Seri and Gua Panjang. About 700 numbers. Led by Dr. H. Keng.

Whitmore, T.C. 1966–1970; visited Langkawi (Kedah), Gua Batu Boh, Gua Musang, Kuala Jenera, Sungei Nenggiri (Kelantan), and Bukit Anak Takun, Bukit Takun, and Gua Batu (Selangor). About 120 numbers.

Wong, Y.K. May 13th 1962; a *Maxburretia rupicola* (Ridl.) Furt. from Bukit Takun, Selangor.

Wooldridge, T.A. June 1896; a *Dracaena curtisii* Ridl. from Langkawi (Kedah).

Wray, L. 1894; two specimens from Perak limestone; labels mutilated, one undated.

Wyatt-Smith, J. June 11th 1960; one *Salacia grandiflora* Kurz. from Gua Batu, Selangor.

Wycherley, P.R. Dec. 28th 1969 (with Stone); Gua Batu, Selangor. Some assorted specimens.

For the purpose of this study most of the limestone areas in Malaya were visited and numerous hills explored and botanised. About 1550 numbers were collected.

The plants treated include the terrestrial as well as the epiphytic members. Included also are species from hill bases where the soil is definitely of limestone origin; this is usually a rusty-red loam and very distinctive. Characteristically there are numerous boulders strewn about. Admittedly it is often difficult to decide what does or does not constitute the limestone vegetation. Certainly the vegetation at hill bases (with limestone derived soil) is different from that on hill tops, but equally it also differs from that of the surrounding lowland forest. This hill base vegetation has arisen as a result of the interaction between the presence of the hill and the surrounding forest. Accordingly I have included the species found here in this treatment.

In the case of plants from the small outcrops recently discovered in Johore (Rajah, 1970) great care was exercised to see that only those actually growing on the rocks were recorded. This is because the outcrops here are very limited and low, from boulder size protrusions to several of about 20 m tall and as broad. Most of the cracks and crevices are filled with soil derived from the surrounding sandstone formation. (This publication also records the first botanical exploration on the Johore limestone.)

All specimens from 'near the base of hill', or from 'hill bases' as recorded on the labels of herbarium sheets are excluded unless the labels also specify that the particular plant was from limestone rock or soil.

In order to obtain as complete a record as possible of the limestone flora, every sheet in the herbaria at the Singapore Botanic Gardens, the University of Singapore and the University of Malaya was scrutinized. A start was also made at the herbarium of the Forest Research Institute but as the search was not showing success it was stopped. Practically all the old and most of the new limestone records there (at Kepong) are duplicated in the Singapore Botanic Gardens herbarium. Subsequently the examination of specimens at Kepong was restricted to the known limestone genera and to recent (post 1960) records from limestone districts (with the help of collector's field notes).

Many labels are unclear and to decide whether a specimen was recorded from limestone or not is not always straightforward. Sometimes the town, village or district bears the same name as the limestone hill (or vice versa), e.g. Baling, Gua Batu and Gua Musang. Specimens in such cases were excluded unless the record states explicitly that it was from the hill.

By searching the herbaria and literature I have managed, I think, to include all the species (possibly with few exceptions) so far recorded from the Malayan limestone.

Purpose and Scope

This work attempts to present a comprehensive account of all pteridophytes (true ferns only) and spermatophytes ever found growing on limestone hills and sites in the Malayan Peninsula. Included also are the non-indigenous species (introduced, inadvertently or otherwise) which have become naturalized and now form part of the wild-growing population.

Sect. 1 discusses the geology, origin and distribution of the limestone hills, the vegetation, phytogeography and size of the flora, and affinities of the floristic components to limestone.

Sect. 2 the flora proper, starts with the Pteridophytes (true ferns only), going on to the Gymnosperms and ending with the Angiosperms (Dictoyledons and Monocotyledons). Under these four main groups, the families are arranged in alphabetical order and thereunder the genera and species. Dichotomous keys leading to the identification of almost all the species are included. For the exceptionally large groups, the Pteridophytes, Euphorbiaceae, Orchidaceae and Rubiaceae, an introductory key with leads to the main key is provided.

Every species is provided with its approved name and the original place of publication. Synonyms, if any, especially those published in major works relevant to the local flora, are cited. References are also made to publications on the local flora, and reference to Henderson (1939) is cited for every species included in his work.

The names of *characteristic species* (those that come under my 'affinity' grouping I and II in ch. 5) are printed in *bold face* type. In addition, brief notes on the distribution, and frequency on the Malayan limestone are often included for these species.

All literature cited in the discussion are listed in full in the bibliography at the end of this work.

Specimens are cited only in special cases, such as rarity, or doubtful locality, or in relation to certain taxonomic problems. However, full lists of specimens are to be found in the dissertation paper, and this may be consulted in the Library of the University of Malaya or in the University Herbarium, Kuala Lumpur.

Lastly Bryophyte collections were made during this study but are not included here because of the difficulty in obtaining identifications. A further study of this group would be desirable.

2. *GEOLOGY, ORIGIN AND DISTRIBUTION OF THE LIMESTONE HILLS.*

Geology

Most of the limestone hills in Malaya rise from flat or undulating plains. They form conspicuous and often spectacular hills up to 2342 ft. (713 m.), (Gua Peningat, Pahang), often with sheer, vertical or overhanging cliffs.

They range in age from Ordovician to Triassic. The estimation of age has been a difficult problem since are recrystallised, unfossiliferous (Hutchison, 1968), and as all studied samples are recrystallised, thermoluminescence cannot be used to differentiate limestone stratigraphically in Malaya (Hutchison, 1968). Up to as late as the 1950's anything calcareous in Malaya has been assumed to be carboniferous and was ascribed to the calcareous formation. Since then many studies have been made, providing a more accurate picture of the age of our limestone, e.g. Paton (1961), Ingham and Bradford (1960), Gobbett (1965a), Hutchison (1968) and Suntharalingam (1968), but the ages of many still remain indicated by only a very rough estimation.

The Kedah/Perlis(including Langkawi) limestone areas are mainly Ordovician-Silurian. The Selangor limestone appears to be confined to the Silurian (Gobbett, 1964), and the recently discovered Johore limestone is Permian (Rajah, 1970). Most of the others are Permian (Paton, 1961), but further studies will probably show a variation in age from the Silurian to Permian (as is the Selangor limestone Paton included under Permian). However no hill has been found to be Triassic which so far is limited to small lenticular beds in Pahang (Paton, 1961).

It is generally thought that the older limestone gives rise to more or less continuous ranges of hills without marked vertical cliffs whereas on the other hand the younger limestone produces more isolated hills with high, vertical or even overhanging cliffs (Paton, 1961). This weathered-look is shown by the Kedah/ Perlis (including Langkawi) limestone of Ordovician-Silurian age. This generalisation was made before the Selangor limestone was known to be Silurian, and now no longer holds. This is because the latter shows marked cliff development (except for Bukit Anak Takun). Thus it would seem that the age of the actual limestone rock itself has little bearing on the development of the hills, and there is no difference in form between hills from Permian and Ordovician-Silurian rock.

Our limestones are generally very pure. Most are white, pale grey or slightly yellowish; some are dark grey to almost black because of carbonaceous or argillaceous impurity. Rarely it is red because of hematite inclusion or by iron staining. Hutchison (1968), who analysed 182 very random samples chemically (which therefore should give a rough indication of the true nature of the Malayan limestone) recorded that most of them have about 2.5% insoluble residue with an arithmetic mean of about 4.4% insoluble residue. He further notes that 81% of his samples are limstone ($CaCO_3$) and 19% dolomite ($CaMg (CO_3)_2$).

Origin

Originally sedimentary, the Malayan limestone is, as mentioned earlier, recrystallised. It is thus in fact marble. This happened when peninsular Malaya underwent an orogeny (an episode of mountain-building during which the rocks, including the Malaysian limestone were compressed, folded and heated) in the Triassic period (about 200 million years ago). Towards the end of the Triassic orogeny the rocks were uplifted into hills and mountains. The botanical stage was set, since then most of the Malayan limestone was never submerged again, and they were ready to receive their first plant. However it is not certain how long it took before the limestone topography as we know came into being.

Various theories have been put forward to explain the existence of the limestone in the form of spectacular karst-tower hills. These are reviewed by Paton (1964), and include block faulting, sub-aerial erosion, folding, marine erosion and plastic flow. The most plausible explanation seems to be simple sub-aerial denudation modified in certain cases by marine erosion.

The theory of sub-aerial erosion takes into account the high solubility of calcium carbonate compared to the majority of the silicates, of which most of all other rocks are composed. This is an important point, for any theory seeking to explain why the limestone hills are in the form they are must also explain why formations of other rocks are not existing in the form the limestone hills are. Weathering of silicate rocks produces more or less rounded topography; on limestone deep channels are often cut.

Streams and swamps at the bases of limestone (assuming that they were once well-jointed and continuous) are highly effective in eroding it. The pH of swamp and stream water in low-lying areas is commonly as low as 3.5 (Paton, 1964). This acidic water gradually erodes the rock, forming channels; floors and walls are enlarged, and from above, downward erosion cuts deep channels that eventually reach the base. The underground channels continue to expand laterally, finally resulting in the collapse of the roofs, producing steep-sided and isolated hills.

The initial stages of erosion by water are evident in the form of grooves or nips, characteristic of many coastal limestone areas in Langkawi and at the bases of hills on the mainland. Some grooves on hills in the Kinta and Kedah/Perlis area are marine in origin, formed in the post-glacial periods (post Pleistocene) when the sea level, at least 50 ft. higher than now (Scrivenor, 1949; Walker, 1956), flooded the plains.

Distribution

Until recently, all the known limestone outcrops were from north of Kuala Lumpur. However in 1965-66, officials of the Geological Survey of Malaysia discovered limestone outcrops in Johore while carrying out geological mapping of that area (Rajah, 1970). The outcrops are in an area 500 by 1200 m on the south-eastern slope of Gunong Sumalayang at an elevation of 250 to 400 m. There are about 30 outcrops here varying in size from boulders 1–2 m across to the largest about 20 m tall and as wide.

Elsewhere in Malaya the limestone hills are in their most spectacular and prolific development in south-west Kelantan and north-west Pahang, in the Kinta valley from Kampar northwards to Ipoh, Tambun and Tanjong Rambutan, and in north-west Perlis.

Hills are also found around Alor Star, Kedah, elsewhere in Pahang, near Kuala Lumpur, Selangor and rarely in Trengganu. They are very prominent in the Langkawi group of islands off the extreme north-west coast of Malaya. Not all the islands are limestone, and some are limestone only in part, but generally limestone is abundant, especially in the eastern and southern aspects of Langkawi. This is the only coastal limestone in Malaya.

The distribution of the Malayan limestone hills is shown in Maps 1, 2 & 3. All the hills botanised are included in the maps except some of the smaller hills which are not named even in regional 1 inch to 1 mile maps. It has also not been possible to include all existing outcrops, but all the limestone localities are represented and most of the popuarly and less popularly known have been included.

3. *VEGETATION*

The limestone vegetation forms a characteristic and easily recognised forest type in Malaya. It is a distinct Edaphic Climax Formation (Symington, 1943). In fact, Corner (1960) considered the limestone forest as one of the three constituent forest types (the other two being the lowland and the mountain forest).

The vegetation supports an extremely diverse and rich flora which is a reflection of the diversity of the habitat. Henderson (1939) classified the Malayan limestone hills into three broad groups, viz.:

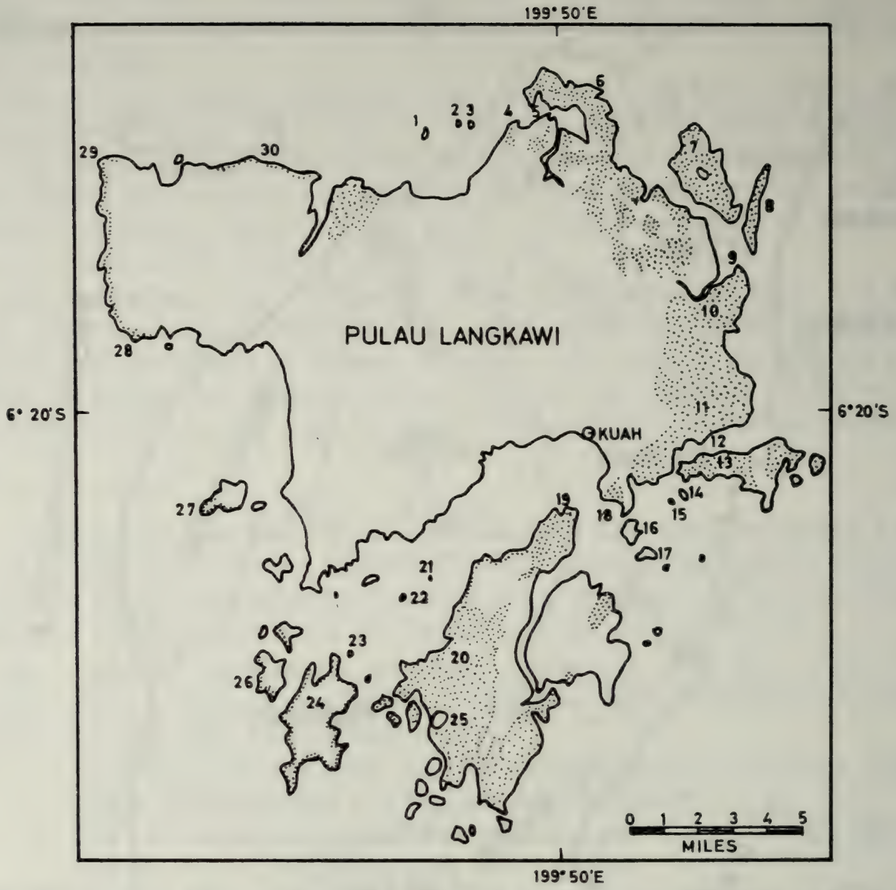
1. Very dry hills with little soil and much exposed rock. Trees usually rather stunted; mosses and herbaceous plants scarce.
2. Wet hills often with gullies filled with rich soil. Trees fair-sized and not stunted; mosses and herbaceous plants present.
3. Soil-rich hills, well covered with soil (usually a stiff red clay), little rock exposed. Trees tall; mosses and herbaceous plants few.

This is in effect, as Henderson further discussed, dividing the limestone hills into two general categories, 'dry hills' (1) and 'wet hills' (2 and 3). This classification however does not do justice in summing up the diverse limestone habitat. 'Dry hills' often have sheltered gullies with soil supporting fair-sized trees, mosses and herbaceous plants. Similarly 'wet hills' often have exposed rocky ridges with stunted vegetation.

Anderson (1965) subdivides the Sarawak limestone habitat into eight groups, viz.: 1. Alluvial soils at the base of hills. 2. Base of hills and ravines between hills. 3. Slopes of hills 4. Cliffs. 5. Scree slopes on hills. 6. Summits of hills at low altitudes. 7. Submontane limestone. 8. Secondary vegetation on hills.

In Malaya there are no submontane limestone hills and this classification does not seem to effectively describe the Malayan limestone habitat. Thus another classification is proposed. This is, like the other schemes, only provisional and there is a great deal of overlap between the subdivisions. This subdivision of the habitat takes into account the geology and topography of the hill, the physiognomy of the vegetation and the floristic composition. Succession is also considered and disturbed or secondary vegetation is therefore made a subdivision.

MAP 1. MALAYA IN GENERAL



MAP 2. LANGKAWI, SHOWING THE MAJOR LIMESTONE LOCALITIES

Key to the numbers (in a clockwise direction starting from the north).

1. Pulau Dangli
2. Pulau Gasing
3. Pulau Pasir
4. Tanjong Batu Kulat
5. Tanjong Ru
6. Gua Cherita
7. Pulau Langgun (with lake)
8. Pulau Tanjong Dendang
9. Tanjong Dagu
10. Tanjong Dagu Forest Reserve
11. Selat Panchor Forest Reserve
12. Selat Panchor (straits)
13. Pulau Timun
14. Pulau Lading
15. Pulau Chupak
16. Pulau Bumbon Besar
17. Pulau Bumbon Kechil
18. Telok Sambar
19. Tanjong Tirai
20. Pulau Dayang Bunting
21. Pulau Jerkom Kechil
22. Pulau Jerkom Besar
23. Pulau Singa Kechil
24. Pulau Singa Besar
25. Tasek Dayang Bunting (lake)
26. Pulau Beras Basah
27. Pulau Rebak Besar
28. Tanjong Belua
29. Tanjong Chinchin
30. Tanjong Tok Manap

The subdivisions are:

1. Base of hills
2. Talus slopes
3. Hill slopes to about 60° steepness
4. Gullies and valleys
5. Cliffs and near-vertical slopes
6. Summits with considerable soil cover
7. Summits with none or very little soil cover
8. Coastal limestone
9. Disturbed areas

Although the nature of the habitat necessitates a classification taking into account all the characteristics present to separate the subdivisions effectively, this classification is more physiognomic than floristic in kind. The physiognomy of the vegetation is in turn dependent on the topography of the hill, the abundance or scarcity of soil, moisture and shelter. The floristic composition however varies a great deal from hill to hill and although it would be possible to subdivide a hill floristically, this pattern of floristic distribution would not hold for other hills. Species characterising a dry rocky summit like Bukit Takun (*Buxus malayana* and *Wikstroemia androsaemifolia*) are not found on a similarly dry and rocky part of, for example, Batu Neng. *Sycopsis dunnii* is common on Bukit Serdam summit (with thin soil) but on Gunong Rapat summit (also with thin soil) a common plant is *Murraya paniculata*, and *Sycopsis dunnii* is absent, and the converse applies.

Floristically also, the limestone north of Alor Star, including those in Langkawi, mainland Kedah and Perlis differs from that further south. They form part of the Thai flora which begins north of Alor Star, in Kedah (Ridley, 1911) or north of the mouth of Kedah river which is near Alor Star (Kloss, 1922). (This difference in the floristic composition is due mainly to the regular dry season from December to February which is confined to the extreme north of Malaya).

However in this classification, the Langkawi limestone is treated in the same manner as the rest and not as a distinct floristic entity. This is in order to provide a coherent picture of the Malayan limestone in which floristic composition is one of the criteria used and not *the* deciding factor.

The examples of plants cited in the following discussion are representative of the subdivisions of limestone habitats in which they are found. However a considerable number of such examples do not have rigid habitat preferences and may also be found in the other subdivisions. Though they are representative of the various subdivisions they are not necessarily found on all hills with similar habitats; in fact many species form very local populations on one or several hills.

1. Base of hills

The bases of hills are usually covered by a mixture of alluvial soil not derived from the limestone but from the surrounding geological formation and also soil derived from weathering of the hills. The vegetation here varies with the locality of the hill and probably with the nature of the derived alluvial soil (from the surrounding geological formation). Protected valleys (wangs) may occur; these are surrounded, often entirely, by abrupt limestone walls. The floor is usually the typical Terra Rossa soil. Such areas are often cultivated (as in the hills around Ipoh).

The vegetation is generally tall and closed, with the crowns of the plants touching or overlapping. Typical species include *Villebrunea sylvatica, Gmelina asiatica, G. villosa, Dendrocnide stimulans, Diospyros cauliflora, Mallotus philippensis, Melanolepis multiglandulosa, Orophea hirsuta* and *Pisonia umbellifera.* Some climbers are also found e.g., *Iodes cirrhosa* and *Mucuna biplicata.*

Sometimes where water drips down from steep rocky slopes or from overhanging cliffs, a distinct herb community develops. Species include *Alocasia lowii, Chirita caliginosa* (which is also found on dry situations) *Epithema saxatile* and *Monophyllaea horsfieldii*. Bryophytes are usually luxuriant.

2. Talus slopes

At and near the base of many hills are accumulations of boulders, organic matter and general debris from the hill. Rocks from this scree have evidently fallen from the hill. Often the bases of hills surrounding amphitheatres or wangs have talus slopes at their bases. These are probably remnants of the roofs of large caverns that have suffered a cave-in. The vegetation here is tall and closed, physiognomically not unlike that on cliff bases (Gp. 1.). The composition is however somewhat different; and perhaps the distinguishing character is the herb and shrub vegetation characteristing such a shady, rocky terrain. The trees and shrubs include *Atalantia roxburghiana* (peculiar to Bukit Takun), *Cleidion javanicum, Morinda elliptica, Streblus ilicifolius* and *Trivalvaria macrophylla*. The herbs include *Heterogonium pinnatum, H. alderwereltii, Impatiens* spp. (I. *mirabilis* dominates the scenery on Pulau Langgun, Langkawi, north of the lake), *Pilea* and *Procris*.

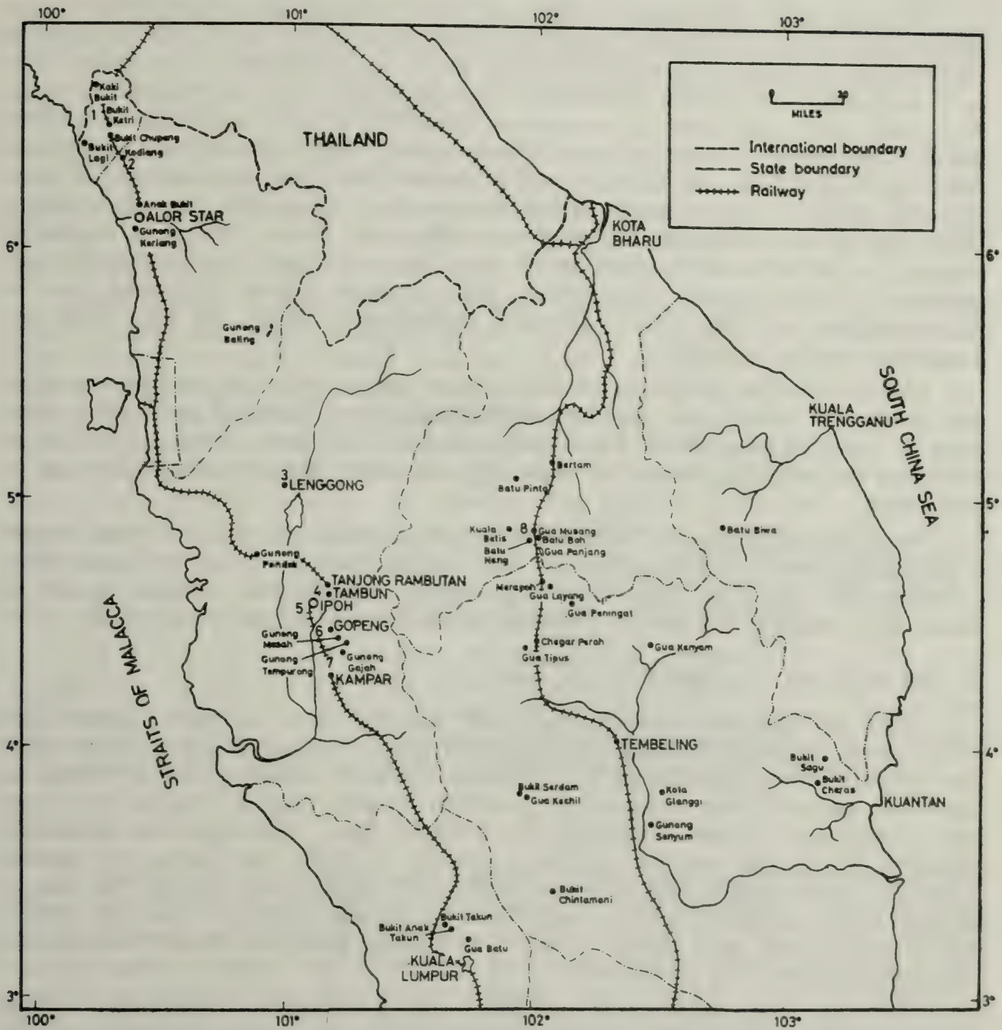
3. Hill slopes to about 60° steep

These more gentle slopes are nearly always covered with soil and support a dense, close vegetation 5–10 m or more tall. The soil may be thin or to about 1 m deep at places, and boulders are usually present emerging from the soil. Ground vegetation is usually spares and is often associated with the boulder outcrops. These include *Antrophyum parvulum* (on rocks), *Ophiorrhiza, Piper*, and in the more sheltered niches *Gymnostachyum decurrens* and *Scutellaria discolor*. The trees and shrubs include *Cladogynus orientalis, Croton cascarilloides, Mallotus dispar, Microdesmis casearifolia, Orophea cuneiformis, Polyalthia brunneifolia, Saraca declinata, S. thaipingensis* and *Rinorea bengalensis*. On Gua Kechil, Raub, the rare tree *Diospyros adenophora* is fairly common.

4. Gullies and valleys

These are often the most sheltered spots on hills. This group includes pot-holes, depressions, gullies, valleys, ravines and other concavities which may be narrow and small or broad and extensive, extending between two peaks on the same hill. The ground is usually deep or shallow soil with a covering of litter and other organic debris. The vegetation is fairly dense, 5–10 m tall with occasional emergents, and physiognomically not unlike that on soil-covered slopes and talus slopes. The floristic composition varies somewhat and its location and topography is usually distinctive. (Sometimes however gullies and valleys may emerge into hill slopes.) Gullies may even be present on the so-called 'dry hills' (the most outstanding example is Bukit Takun), harbouring mosses and delicate herbaceous plants like *Corybas mucronatus* and *Goodyera hispida*. The ground vegetation is usually quite sparse, no doubt because of the closed canopy. Bryophytes are common and herbs like *Epithema saxatile* and *Monophyllaea* are usually associated with boulder outcrops.

The trees and shrubs include *Agrostistachys gaudichaudii, Canthium didymum, Fagraea curtisii, Randia densiflora, Sauropus suberosus* and *Sterculia rubiginosa*. Climbers like *Connarus* and *Lasiobema* are found and the palms present include *Arenga westerhoutii* (also from talus slopes), *A. hookeriana* and *Iguanura polymorpha*.



MAP 3. MALAYA (EXCLUDING LANGKAWI) SHOWING THE MAJOR LIMESTONE OUTCROPS

Key to the numbers indicating position of outcrops.

1. Bukit Besih Hangat
   Bukit Wang Tangga
   Tebing Tinggi
2. KODIANG — including Batu Hantu
   Batu Kalong
3. LENGGONG — including Batu Tukang
   Gua Badak
   Gua Pipit
   Gua Putri
4. TAMBUN — including Gunong Ginting
   Rotan Segar
5. IPOH — including Perak Cave Temple
6. GOPENG — including Gunong Lanno
   Gunong Rapat
7. Kuala Dipang
   Sungei Siput
8. GUA MUSANG — including Batu Machang
   Batu Papan
   Batu Tapah
   Gua Serai

5. Cliffs and near-vertical slopes

Vertical cliffs, overhanging cliffs and near vertical slopes present a unique habitat and support a distinct vegetation which depends on the degree of exposure of the cliffs, presence or absence of soil pockets and availability of moisture. This is a very easily recognised subdivision topographically and the vegetation varies from very sparse and open (or sometimes absent) to a fairly dense herb and scrub cover. This denser vegetation cover is found along ledges where there is accumulated soil and debris and in other soil pockets. Where there is seepage or water dripping down a characteristic vegetation develops along this line of moisture. This may be on overhangs or clefts on cliff faces. If on clefts this vegetation decends to the base of the cliff and is very similar to that described under subdivision 1 (where water is available). This includes *Chirita, Epithema saxatile, Monophyllaea* and the fern *Adiantum malesianum* (which is also from dry localities) and bryophytes.

Cliff faces with no cracks or crevices do not support any macro-vegetation, but those with cracks and crevices which invariably collect soil and other debris support a distinctive flora. The species include the very characteristic *Boea, Paraboea* and *Chirita. Boea* spp. especially are often very prominent high up on cliff faces.

Near vertical slopes and cliffs with ledges and other soil pockets often support a herbaceous or scrubby vegetation. The species include *Canscora pentanthera, Cymbopogon calcicola, Callicarpa angustifolia, Cheilanthes farinosa* (only on Bukit Chintamani), *Jasminum, Pyrrosia stigmosa* and *Zizyphus oenoplia.*

6. Summits with considerable soil cover.

Most hill summits are covered with soil (at least in part). Some have considerable to extensive rock outcrops with sparse vegetation (these rocky spots are included under subdivision 7.) In places scattered boulders and pot-holes are common; generally the topography is uneven to very rugged. Ridges with some soil supporting a closed vegetation are included here. The vegetation is usually scrubby, 2–7 m tall and the canopy is closed. In places the plants are spindly. Generally these shrubs and trees are fairly well spaced, and though the canopy is closed there usually is a rich ground flora. Occasional emergent trees are present, eg; *Mangifera* sp. on Gunong Pondok, *Madhuca ridleyi* on Bukit Serdam and *Garcinia murdochii* on Gua Kechil.

The trees (they are usually somewhat stunted, though not extremely so) and shrubs include *Cleistanthus gracilis, Decaspermum fruticosum, Dehaasia curtisii, Eriobotrya bengalensis, Erythroxylum cuneatum, Eugenia pendens, Garcinia minutiflora, Mallotus brevipetiolatus, Mallotus miquelianus, Murraya paniculata, Neolitsea zeylanica* and *Sycopsis dunnii* (especially on Bukit Serdam). The pandan, *Pandanus irregularis* is common and conspicuous on ridges on Batu Neng. Climbers and scramblers are usually scarce and include *Maytenus curtisii* and *Lygodium polystachyum.*

The ground vegetation is fairly rich in bryophytes especially in the more sheltered spots on rocks and at the basal parts of tree trunks. The herbs include the lycopod, *Lycopodium squarrosum;* ferns are common and in places from the dominant ground cover; they include *Asplenium adiantoides, A. macrophyllum, Loxogramme avenia, Photinopteris speciosa, Phymatodes scolopendria* and *Pyrrosia stigmosa.* Ground orchids are equally common and include *Agrostophyllum bicuspidatum* (which may also be a low epiphyte), *Coelogyne asperata* (which on parts of Batu Neng and Batu Tapah forms almost pure mats), *Dendrobium luxurians, Eria rigida* and *Renanthera histrionica.* Epiphytes are usually not conspicuous though occasionally they are found; these include orchids, e.g. *Appendicula torta* and *Bulbophyllum apodum* and ferns, e.g. *Pyrrosia.*

7. Summits with no or very little soil cover

Most hills have some exposed rocky parts, while a very few have extensive rocky summits. Soil is scanty and found in little hollows, cracks and clefts in the rock but is never completely absent. Even extensively rocky summits have gullies and valleys where soil and litter are accumulated and the vegetation supported is different (included under subdivision 4.)

The vegetation on these rocky summits is sparse and open but fair-sized trees rooted in clefts and hollows are present. Most are, however, stunted and gnarled though occasionally large ones occur. An example are the figs, the roots of which ramify all over the rocks, into every crack and crevice and often extending for many meters over cliff faces in an intermeshed network.

Bukit Takun in Selangor is the classic example of a hill with an extensive rocky summit, but other examples occur, e.g. in Langkawi. The plants on these hills include some herbs usually from soil pockets and from amongst the surface roots of trees where some debris have accumulated. These include *Adenia nicobarica, Amorphophallus* spp., *Arisaema fimbriatum, A. roxburghii, Boea* spp., *Chirita* spp. and *Dichanthium mucronulatum*. It is interesting to note that of these, *Adenia nicobarica, Amorphophallus* spp. and *Arisaema* spp. have fleshy tubers which often grow into cracks and crevices. The possession of tubers could be an advantage under such dry and exposed conditions. Climbers present include *Dischidia hirsuta, Morinda umbellata* and *Secamone micrantha*, and the pandan, *Pandanus alticola* (commonly an epiphyte outside the limestone field) which is often present growing from rocks (it is abundant on Bukit Takun).

The trees and shrubs present include *Buxus malayana, Diospyros ferrea* (commonly on hills around Gua Musang), *Ficus calcicola, Glycosmis calcicola, Memecylon laevigatum, Pistacia malayana, Planchonella obovata, Podocarpus polystachyus, Tarenna curtisii, Terminalia triptera* (only Langkawi), *Vaccinium littoreum* (only on Bukit Takun and Anak Takun), and *Vitex siamica*.

8. Coastal limestone

In Malaya this only occurs in Langkawi where part of the coast of the main island and many of the smaller islands are entirely limestone. Hills and islets which descend gradually to the sea are often fringed on the seaward edge by narrow sandy beaches (non-limestone, and derived from other geological formations as weathered limestone produce hardly any 'sand') on which develops a typical strand vegetation. It is these low limestone areas that are mostly influenced by the sea and are invaded by some species from the strand vegetation. Hills with tall abrupt cliffs do not show any littoral influence. However, it must be remembered that many species from the Langkawi limestone are not found on limestone further south on the mainland, but this is due to the northerly position of Langkawi principally, and not due to littoral influence (which is coincidental and at the most contributary). These species include *Bombax anceps, Cycas siamensis, Colona merguensis, Euphorbia antiquorum, Grewia viminea, Hopea ferrea, Pentacme siamensis, Sterculia lancaviensis* and *Vatica cinerea*.

The coastal limestone therefore is restricted to that part of the limestone in close proximity to the sea, and this is usually near sea-level. The seaward edge is fringed with sand which supports a typical Indo-Malaysian littoral vegetation (sensu Schimper, 1903). The vegetation on this limestone is sparse to dense, short or tall, depending on the availability of soil and the topography; but littoral species are present. The species include some herbaceous members like *Davallia solida, Humata pectinata, Eurycles sylvestris* and *Tacca leontopetaloides*. Trees and shrubs include *Barringtonia asiatica, Caesalpinia crista, Guettarda speciosa,* *Heritiera littoralis, Pandanus odoratissimus, Peltophorum pterocarpum, Thespesia populnea* and *Xylocarpus granatum.* Together with the species mentioned above this makes up a distinctive coastal limestone vegetation (probably distinctive even if there were other coastal limestone areas further south).

9. Disturbed areas

Disturbed areas usually occur on the summits, lower slopes and bases of hills. These disturbances could have been brought about by a number of causes, viz:

(i) Fire, occurring naturally or artificially, e.g. Bukit Takun in August 1970 and Gua Musang in mid-1969.

(ii) Mining and quarrying activities. This is seen on a large number of hills in all the major limestone districts.

(iii) Agriculture, affecting only hill bases, e.g. some hills around Ipoh and in limited spots on many other hills.

(iv) Erection of communication transmitters and trignometrical stations, e.g. on Gunong Lanno, G. Layang-Layang and G. Tasek, also on other hills.

(v) Frequent trampling by visitors, e.g. on Bukit Takun and Gua Musang.

Whatever the cause, disturbances result in the partial or complete destruction of the original vegetation. It is interesting to note that *Cratoxylum maingayi, Podocarpus polystachyus* and *Radermachera lobbii* survived the 1969 fire on Gua Musang that destroyed all the other vegetation affected. *Cratoxylum* and *Podocarpus* probably survived because they were the largest trees there and consequently had thick bark. Several plants of *Radermachera* (they were slender and probably not more than 4 m tall) were burnt almost to the ground. By August 1971 the sucker-shoots sent out were already 2 m tall and flowering.

Though the complete development from sere to high forest has never been observed, a composite and representative picture (at least of the initial stages) can be formed by observation of a number of hills. One of the earliest colonisers is the moss *Bryum coronatum* Schwaegr. which was abundant on Gua Musang in August 1970 and also in August 1971 on burnt earth and on rocks. This moss is followed (or accompanied) by a large number of ubiquitous weeds, truly opportunistic and very adaptable and probably completely indifferent to the limestone influence. The species include *Chrysopogon aciculatus, Colocasia gigantea* (prominent on Gua Musang), *Eleusine indica, Erechtites valerianifolia, Eupatorium odoratum, Macaranga tanarius, Muntingia calabura* (prominent on the quarried slopes of Bukit Chintamani), *Nephrolepis biserrata, Neyraudia reynaudiana* (conspicuously gracing the summit of Gua Musang in 1971), *Paspalum conjugatum, Pityrogramma calomelanos, Pteridium caudatum* var. *yarrabense, Pteris vittata, Rhynchelytrum repens* and *Solanum ferox.* Limestone elements present at this early stage include *Boea* spp., *Chirita* spp. and *Schizaea inopinata.*

Trees like *Macaranga tanarius* and *Trema* spp. are probably quite persistent, though the latter stages of this succession have not been observed. Presumably seedlings of other limestone elements get established and eventually from the dominant vegetation once again, shading out the colonisers.

4. *PHYTOGEOGRAPHY AND SIZE OF THE FLORA*

The total number of species recorded for the limestone flora is 1216 distributed in 582 genera and 124 families (This includes the true ferns, Gymnosperms and Angiosperms). The introduced elements (as weeds and escapes from cultivation) number 39 species or 3.2% of the total flora.

The breakdown of the flora is as follows:

		Genera	*Species*	*Dubious Records*
PTERIDOPHYTES				
Adiantaceae		8	16	—
Dennstaedtiaceae		17	45	—
Grammitidaceae		1	2	—
Hymenophyllaceae		1	4	—
Polypodiaceae		11	21	—
Schizaeaceae		2	3	—
Thelypteridaceae		3	6	—
TOTAL	7	43	97	—
GYMNOSPERMS				
Araucariaceae		1	1	—
Cycadaceae		1	2	—
Gnetaceae		1	2	—
Podocarpaceae		1	2	—
TOTAL	4	4	7	—
ANGIOSPERMS				
DICOTYLEDONS				
Acanthaceae		16	32	—
Amaranthaceae		2	2	1
Anacardiaceae		8	9	1
Annonaceae		19	39	—
Apocynaceae		10	17	—
Aquifoliaceae		1	1	—
Araliaceae		3	9	—
Aristolochiaceae		—	—	1
Asclepiadaceae		9	23	—
Balanophoraceae		1	1	—
Balsaminaceae		1	8	—
Begoniaceae		1	8	—
Bignoniaceae		1	1	—
Bombacaceae		2	2	—
Boraginaceae		2	3	—
Burseraceae		3	5	—
Buxaceae		1	3	—
Caprifoliaceae		1	2	—
Capparidaceae		1	1	—
Cardiopteridaceae		1	1	—
Celastraceae		6	10	—
Chloranthaceae		1	1	—
Combretaceae		3	5	—
Compositae		7	9	—
Connaraceae		2	3	—
Convolvulaceae		4	5	—
Cucurbitaceae		6	6	—
Datiscaceae		1	1	—
Dilleniaceae		3	3	—
Dipterocarpaceae		8	12	—
Ebenaceae		1	17	—
Elaeocarpaceae		1	1	—

Dicotyledons (*cont.*)				
Ericaceae		2	2	—
Erythroxylaceae		1	1	—
Flacourtiaceae		37	81	—
Fagaceae		1	2	—
Eacourtiaceae		5	12	1
Gentianaceae		3	3	—
Gesneriaceae		11	39	—
Guttiferae		4	11	—
Hamamelidaceae		2	2	—
Hernandiaceae		1	1	—
Hypericaceae		1	1	—
Icacinaceae		2	3	—
Labiatae		8	13	—
Lauraceae		8	13	—
Lecythidaceae		1	3	—
Leguminosae		10	31	3
Lentibulariaceae		1	1	—
Loganiaceae		3	8	1
Loranthaceae		4	5	—
Lythraceae		1	1	—
Malvaceae		4	4	—
Melastomaceae		8	18	1
Meliaceae		6	8	—
Menispermaceae		6	6	—
Monimiaceae		1	1	—
Moraceae		3	29	—
Myristicaceae		2	5	—
Myrsihaceae		4	21	—
Myrtaceae		4	9	—
Nepenthaceae		1	1	—
Nyctaginaceae		2	3	—
Ochnaceae		1	1	—
Oleaceae		3	11	—
Onagraceae		1	1	—
Oxalidaceae		1	1	—
Passifloraceae		2	2	—
Piperaceae		3	14	—
Pittosporaceae		1	1	—
Polygalaceae		3	5	—
Polygonaceae		1	1	—
Primulaceae		1	1	—
Ranunculaceae		1	2	—
Rhamnaceae		4	5	—
Rhizophoraceae		1	1	—
Rosaceae		2	2	—
Rubiaceae		27	66	—
Rutaceae		8	14	1
Santalaceae		1	1	—
Sapindaceae		4	4	—
Sapotaceae		6	8	—
Scrophulariaceae		3	4	—
Solanaceae		2	6	—
Staphyleaceae		1	1	—
Sterculiaceae		8	13	—
Thymelaeaceae		1	3	—
Tiliaceae		4	7	—
Ulmaceae		2	3	—
Urticaceae		9	12	—
Verbenaceae		8	14	—
Violaceae		1	4	—
Vitaceae		6	19	1
TOTAL	93	389	805	11
	=	=	=	=

MONOCOTYLEDONS				
Agavaceae		1	7	—
Alismataceae		—	—	1
Amaryllidaceae		2	2	—
Araceae		19	43	1
Burmanniaceae		2	3	—
Commelinaceae		4	7	1
Cyperaceae		4	13	—
Dioscoreaceae		1	10	—
Flagellariaceae		1	1	—
Gramineae		26	32	1
Hypoxidaceae		1	1	1
Liliaceae		4	5	—
Lowiaceae		1	1	—
Marantaceae		2	2	—
Musaceae		1	1	—
Orchidaceae		52	136	—
Palmae		12	18	—
Pandanaceae		1	6	—
Stemonaceae		1	1	—
Taccaceae		1	1	—
Triuridaceae		1	1	—
Zingiberaceae		9	16	—
TOTAL	22	146	307	5
GRAND TOTAL	126	582	1216	16

The total number of families presented here include Aristolochiaceae and Alismataceae which have only been dubiously recorded. Thus the number of families actually recorded from the limestone is 124. The total number of plants recorded from limestone is 1216 and excluding the ferns this give a total of 1119 species of spermatophytes. Keng (1970) estimated that between 8000-8500 species of spermatophytes occur in the Malay Peninsula. Thus the total number of species of spermatophytes on the limestone is between 13.0–13.9% of the total number of species found in the Peninsula.

Henderson (1939) compared the number of species on limestone and the area of limestone with the total number of species in Malaya and the total area of Malaya. Based on Scrivenor, in Burkill (1935), Henderson concluded that the total area of limestone, which is about 260 sq. km. (100 sq. miles), is 0.2–3% of the total area of the Peninsula. The total number of species from limestone recognised then was 745 which was about 8–9% of the total number of flowering plants (then known) in the Peninsula. These figures seem to indicate a much richer flora per unit area on the limestone than on the other formations. The present figure of 13.0–13.9% would suggest an even richer flora.

This method of comparison assumes that there is a direct relationship between the number of species and the area of land, and that the number of species increases linearly with the increase in land area. This seems incorrect. For instance, Gua Batu supports about 170 species of plants. This is 14.5% of the total number recorded from limestone. It has an area of only about 2.59 sq. km. (1 sq. mile), which is 1% of the total area of limestone in Malaya. It would appear that Gua Batu were floristically 14.5 times richer than the other limestone hills.

To obtain a correct picture, only the 'minimal area' of a community should be used in comparison with the 'minimal area' of another community. This concept of 'minimal area' (Braun-Blanquet, 1932; Poore, 1955) has been defined as the smallest area which can contain an adequate representation of an association. However, the 'minimal area' for both the limestone and the lowland forest in Malaya have not been worked out. One alternative, therefore, is to select an area with the same or about the same area as the limestone and whose flora has been worked out. This flora could be used to compare the limestone flora with.

The flora of Penang island which is about 285 sq. km. (110 sq. mi.) in area has been worked out by Curtis (1894). His list of flowering plants total 1805 species. Similarly the flora of Singapore (Ridley, 1900) which is about 582 sq. km. (225 sq. mi.) included 1952 species. The two floras give an idea of the richness of the Malayan flora but as far as a comparison with the limestone flora go, they do not give an accurate picture. The limestone flora is from an edaphic climax formation whereas areas like Singapore and Penang support (originally) a climatic climax formation which includes a number of other climaxes, e.g.; mangrove swamp forest, beach forest, hill dipterocarp forest (in Penang), *Adinandra* forest (in Singapore), riparian fringes and seasonal swamp forest (at least in Singapore) apart from the lowland dipterocarp forest.

The other alternative therefore is to compare a "minimal area" of the limestone flora with the "minimal area" of the flora of another edaphic climax formation. This comparison will probably give the most accurate picture of the relative size and richness of the limestone flora. Unfortunately no flora of any other edaphic climax in Malaya has been worked out that could be conviniently used.

However, Anderson (1963) published an account of the past swamp forest of Sarawak and Brunei, which under the present circumstances should be the most relevant to compare the limestone flora with. The coastal and deltaic peat swamps cover a total of 15644 sq. km. (6040 sq. mi.) of Sarawak and Brunei. The total number of flowering plants recorded in Anderson's list is 393 species. Thus in comparison even the vastness of the Sarawak and Brunei peat swamps have not support a flora as rich as that on the Malayan limestone. The limestone vegetation of Sarawak (surface area much less than the peat swamp) is also exceptionally rich in plant species. A preliminary report on the Sarawak limestone (Anderson, 1965) records over 600 species, and this number is bound to increase as more limestone areas are explored.

Thus one can conclude that the limestone flora of Malaya (and Sarawak) is extremely rich in species, intrinsically and also relatively, in comparison with the peat swamp flora of Sarawak and Brunei, and most probably with floras of other edaphic climaxes.

The total number of families recorded from limestone is 124; of these 117 are families of spermatophytes. The total number of families of flowering plants recorded from Malaya (both native and introduced) is 188 (figure obtained by totalling the list in Keng, 1969). The delimitation of families in this study is the same as in Keng except for Icacinaceae, which is split into Cardiopteridaceae and Icacinaceae, and Tiliaceae which has been treated as Elaeocarpaceae and Tiliaceae. With the addition of these two families the total number of plant families in Malaya becomes 190; the total recorded from limestone amounts to 61.6% of this.

This rich flora differs from that of the rest of Malaya only in degree and not in kind (Henderson 1939). No one family or group of families predominates or is confined to the limestone except for two small families represented by very few species in Malaya, Buxaceae (three species) and Primulaceae (one species). The representation of a family on the limestone also more or less reflects the size of the family as represented in Malaya. Table 1 shows the twelve largest families in Malaya (from Keng, 1969) which is based on Ridley, 1925, with the total genera and species from limestone compared beside them.

TABLE 1. GENERA AND SPECIES IN THE TWELVE LARGEST (SPECIESWISE) FAMILIES IN MALAYA AND THEIR OCCURRENCE ON LIMESTONE

Families	Genera		Species	
	Malaya	Limestone	Malaya	Limestone
Orchidaceae	104	52	669	136
Rubiaceae	67	27	368	66
Euphorbiaceae	71	37	343	81
Leguminosae	66	19	266	31
Gramineae	83	26	205	32
Annonaceae	30	19	184	39
Palmae	30	12	181	18
Melastomaceae	25	8	174	18
Lauraceae	16	8	174	13
Acanthaceae	36	16	168	32
Gesneriaceae	21	11	161	39
Zingiberaceae	20	9	157	16
Averages: Ratio	2 :	1	6 :	1

On limestone, Orchidaceae still tops the list but there are proportionally more members of the Euphorbiaceae than Rubiaceae. The limestone seems a little poor in Leguminosae, Palmae, Melastomaceae, Lauraceae and Zingiberaceae though the other families are more or less proportionally represented. The reasons for this difference may be various and not conjectured as knowledge on the requirements of these plants is almost non-existent.

The families recorded from Malaya but not represented on the limestone are:

GYMNOSPERMS

Pinaceae

Dicotyledons

Aceraceae
Actinidiaceae
Aizoaceae
Ancistrocladaceae
Basellaceae
Bixaceae
Cactaceae
Campanulaceae
Caricaceae
Caryophyllaceae
Casuarinaceae
Chenopodiaceae
Clethraceae
Cornaceae
Crassulaceae
Cruciferae
Cunoniaceae
Daphniphyllaceae
Dichapetalaceae
Droseraceae
Elaeagnaceae
Epacridaceae
Gonystylaceae
Goodeniaceae
Hydrophyllaceae
Illiciaceae
Juglandaceae
Linaceae
Magnoliaceae
Malpighiaceae
Monotropaceae
Moringaceae
Myricaceae
Nymphaeaceae
Olacaceae
Opiliaceae
Orobanchaceae
Pedaliaceae
Plantaginaceae
Plumbaginaceae
Portulacaceae
Proteaceae
Rafflesiaceae
Sabiaceae
Salicaceae
Saxifragaceae
Schisandraceae
Simaroubaceae
Stylidiaceae
Styraceae
Symplocaceae
Theaceae
Turneraceae
Umbelliferae

Monocotyledons

Bromeliaceae
Butomaceae
Cannaceae
Eriocaulaceae
Hydrocharitaceae
Iridaceae
Juncaceae
Lemnaceae
Najadaceae
Philydraceae
Pontamogetonaceae
Pontederiaceae
Restionaceae
Smilacaceae
Typhaceae
Xyridaceae

These 71 families can be divided into six groups.

1. Aquatic or marsh plants. These are represented by 12 families, and include most of the monocots. They are, Nymphaeaceae, Stylidiaceae, Butomaceae, Eriocaulaceae, Hydrocharitaceae, Lemnaceae, Najadaceae, Philydraceae, Pontamogetonaceae, Pontederiaceae, Restionaceae, and Typhaceae.

2. Parasitic plants. These are represented by two families, Orobanchaceae and Rafflesiaceae.

3. Coastal plants. Represented by three families, Casuarinaceae, Goodeniaceae and Portulacaceae. Aizoaceae also has a coastal member in *Sesuvium*, while the remaining two genera in Malaya are not very common herbs.

4. Weeds or plants in cultivation. These are represented by 17 families, Pinaceae, Basellaceae, Bixaceae, Caricaceae, Caryophyllaceae, Cactaceae, Chenopodiaceae, Crassulaceae, Cruciferae, Moringaceae, Pedaliaceae, Plantaginaceae, Plumbaginaceae, Salicaceae, Turneraceae, Bromeliaceae and Iridaceae.

5. Very rare plants. In many cases these families are represented by a solitary species in Malaya. There are 15 such families. They are, Aceraceae, Ancistrocladaceae, Clethraceae, Cunoniaceae, Daphniphyllaceae, Droseraceae, Elaeagnaceae, Epacridaceae, Hydrophyllaceae, Illiciaceae, Magnoliaceae, Monotropaceae, Myricaceae, Cannaceae and Juncaceae.

6. Others. These remaining 23 families are often small and uncommon. They are Actinidiaceae, Aizoaceae, Campanulaceae, Cornaceae, Dichapetalaceae, Gonystylaceae, Juglandaceae, Linaceae, Malpighiaceae, Olacaceae, Opiliaceae, Proteaceae, Sabiaceae, Saxifragaceae, Schisandraceae, Simaroubaceae, Styracaceae, Symplocaceae, Theaceae, Umbelliferae, Smilacaceae and Xyridaceae.

It is unlikely that members of group 1 will ever be found on limestone, but it is probable that members of group 2 are present on limestone. Members of group 3 could conceivably be present on coastal limestone barring any physiological antagonism to limestone. When more limestone areas are disturbed by man, some, particularly the weed members of group 4 will probably be recorded. Members group 5 which are very rare plants will, even if they are recorded on limestone, also be very rare. New records for limestone from families not yet represented will therefore most likely be from group 6, but there will not be many species, for most of these families are small. The greatest number of new records will probably be from families already represented on the limestone.

Phytogeography

The 1216 species recorded from the limestone can be grouped according to their geographical distribution into a number of classes, viz:

PANTROPIC: Species occurring throughout the tropical regions of the world.

PALEOTROPIC: Species occurring in the tropics of the Old World, from Africa and India through Malesia and to the Pacific.

INDO-MALESIAN: Species disturbed in mainland Asia as well as in Malesia; including India to the Himalayas, Burma, S. China, Indochina, Thailand, Malesia and southwards to Australia and the Pacific Islands.

ASIATIC: Species only in mainland Asia, sometimes only from Thailand.

MALESIAN: Species occurring in Malesia, including Malaysia, Indonesia, Philippines, New Guinea and sometimes to Australia and the Pacific.

ENDEMIC: Species occurring only in Malaya. These are subdivided into
(a) Species restricted to limestone in Malaya.
(b) Species not restricted to limestone in Malaya.

The result of this analysis is shown in Table 2.

TABLE 2. GEOGRAPHICAL DISTRIBUTION OF THE SPECIES
NUMBER OF SPECIES

	Pterido-phytes	Gymno-sperms	Angio-sperms	Total	%
PANTROPIC	6	—	14	20	1.7
PALEOTROPIC	8	—	27	35	2.9
INDO-MALESIAN	40	4	315	359	29.6
ASIATIC (Asia mainland)	5	1	228	234	19.0
MALESIAN	32	1	225	257	21.2
ENDEMIC (total)	5	—	266	272	22.5
(a. restricted to limestone	2	—	127	129	10.7)
(b. not restricted to limestone	3	—	139	143	11.8)
WEEDS AND ESCAPES	1	—	38	39	3.2

From the table it can be seen that the pantropic element is negligible; this is because most species of this group are weeds (plants that occur in cultivated habitats as undesirables, also in lawns and other open places and often as members of secondary vegetation) and have been included under that group. The widely distributed paleotropic element is also small. There is no predominance of either the Asiatic or Malesian element, both being equally represented except for the ferns. The weeds and escapes are noticably few in number; this is probably because there are few areas on the limestone that support a secondary vegetation. However, this is not to say that the limestone hills have been free from interference, but, that when the limestone hills are disturbed it usually means that the habitat itself is bodily removed as for instance in mining and quarrying.

Krasan (1882) and Steenis (1934) suggested that on limestone mountains plants might be able to descend abnormally low. Although there are no really high limestone mountains in Malaya this tendency can be seen. Here the mountain massif has many peaks rising to over 1500 m, with Gunong Tahan rising to 2187 m. Plants known from 800–2000 m (very rarely from lower elevation, if ever) have been found on low elevation (usually less than 300 m) on the limestone and not elsewhere.

The species recorded include *Antrophyum semicostatum, Leptochilus decurrens, Vittaria angustifolia, Alyxia angustifolia, Alyxia pumila, Corybas, mucronatus, Distylium stellare, Liparis compressa. Paphiopedilum lowii, Schefflera elegans, Sciaphila asterias, Scycopsis dunnii* and *Toxocarpus curtisii.*

5. *AFFINITIES OF THE FLORISTIC COMPONENTS TO LIMESTONE*

The component species of the Malayan limestone can be arranged in the following four groups:

I. EXCLUSIVES: These are species which, in Malaya, are restricted to the limestone and include, (a) Species endemic to Malaya. (b) Species not endemic to Malaya.

II. PREFERENTS: Species with a preference for the limestone field, appearing in both fields (limestone and non-limestone) but more abundantly in the limestone field.

III. INDIFFERENTS: Species with no affinity for either field, appearing in both fields without exhibiting any difference in abundance between them. This group includes most epiphytes and plants of secondary vegetation.

IV. STRANGERS: Species appearing accidentally on the limestone field; frequently collected from the non-limestone field but only rarely from the limestone field.

The criterion of fidelity (Brown-Blanquet, 1932) is used in constructing this grouping, fidelity being indicative of the degree with which a species is restricted to a particular kind of community (in this case the limestone community).

The fidelity of each species and thus the allocation to the various groups is based solely on field work. Species under groups I and II are termed the characteristic species.

Rarely collected species which have been recorded both from limestone and non-limestone fields are included under group III (indifferents) instead of under group IV (strangers). This is because the limestone areas are probably the least botanised of all the vegetation types in Malaya and chances are that rare species already recorded from limestone are more likely to turn up from it again rather than from the other vegetation types.

Weeds and plants escaped from cultivation usually fit into groups III (indifferents) or IV (strangers). However, here they are listed separately.

The true and intrinsic reasons for a plant to be on the limestone field could also be used to classify the floristic components. Any of the plants found on limestone could be:

(a) Calciphilous (chalk-loving) in the true physiological sense (Jackson, 1928). They may be obligate calciphiles, in which case the limestone field is a prerequisite for growth and survival, or non-obligate. The non-obligates have a physiological need or affinity for limestone but are able to survive without the limestone field.

A large number of species in my group I (exclusives) are probably obligate calciphiles while some (those that are non-endemic which are also found away from the limestone outside Malaya) are probably non-obligate calciphiles. These non-obligate calciphiles will also include a large number of species from my group II (preferents).

(b) Indifferents; species that are able to tolerate or are unaffected, physiologically, by the limestone habitat; as in my group III.

(c) Calcifugal (shunning chalk) in the true physiological sense (Jackson, (1928). Obligate calcifuges cannot tolerate the limestone field whereas the non-obligate calcifuges may often appear as strangers on the limestone field when the other criteria of space, competition and moisture are favourable. The non-obligates include at least some of my group IV.

However, this classification can only be effected by experimental work.

The species list of the different groups follows and are summed up in Table 3.

I. EXCLUSIVES

PTERIDOPHYTES

Adiantum zollingeri
Antrophyum parvulum
Cheilanthes farinosa
*Doryopteris allenae
Doryopteris ludens
Drynaria bonii
Heterogonium alderwereltii
Heterogonium pinnatum
Lygodium polystachyum
Nephrolepis dicksonioides
*Polystichum lindsaeifolium
Pyrrosia stigmosa
Schizaea inopinata
Tectaria amplifolia
Tectaria devexa

GYMNOSPERMS

Cycas siamensis

ANGIOSPERMS

DICOTYLEDONS

Actephila excelsa
Aeschynanthus longicaulis
*Amaracarpus saxicola
Andrographis tenuiflora
*Aporuellia sumatrensis var. ridleyi
*Adisia biflora
*Ardisia langkawiensis
*Ardisia meziana
Argostemma diversifolium
*Barleria siamensis var. glabrescens
Begonia curtisii
*Begonia foxworthyi
*Begonia ignorata
*Begonia kingiana
*Begonia nurii
*Begonia phoeniogramma
Boea acutifolia
*Boea brachycarpa
*Boea caerulescens
*Boea divaricata
*Boea lanata
*Boea minutiflora
*Boea paniculata
*Boea parviflora
*Boea suffruticosa
Boea treubii
*Boea verticillata
Boerhavia chinensis
*Buxus holttumiana
*Buxus malayana
*Buxus rupicola
*Callicarpa angustifolia
*Canarium perlisanum
Canscora pentanthera
*Canthium aciculatum
Capparis diffusa
Celtis philippensis
*Chirita caliginosa
Chirita hamosa
Chirita involucrata
Chirita lacunosa
*Chirita rupestris
*Chirita sericea
*Cleistanthus parvifolius
Cnesmone laevis
*Cnesmone subpeltata
Colona javanica
Cynoctonum mitreola
Dendronide sinuata
Dichiloboea speciosa

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*Endemic to Malaya.

Dicotyledons (*cont.*)

*Dicliptera rosea
Dimocarpus longan ssp. longan var. longan
Diospyros daemona
*Diospyros holttumii
Diospyros retrofracta
Diospyros transitoria
Diospyros undulata
*Dischidia tomentella
*Drypetes nervosa
*Embelia calcarea
Euphorbia antiquorum
Excoecaria oppositifolia
*Fagraea calcarea
Ficus calcicola
Garuga floribunda
Glossocarya mollis
*Glycosmis calcicola
*Glycosmis calcicola var. kelantanica
Glyptopetalum zeylanicum
*Gongylosperma lanuginosum
Goniothalamus subevenius
Grewia viminea
Gymnanthera insularum
*Gymnostachyum robinsonii
Heritiera pterospermoides
*Homalium kunstleri
Homalium undulatum
*Hoya occlusa
Hydnocarpus ilicifolia
*Impatiens crytoneura
Impatiens marosepala
Impatiens mirabilis
Impatiens opinata
*Impatiens ridleyi
Impatiens scortechinii
*Impatiens tipusensis
Impatiens vaughanii
*Isonandra perakensis var. kelantanensis
*Isonandra perakensis var. perakensis
*Jasminum cordatum
*Jasminum curtisii
*Jasminum sp. A aff. trinerve
*Jasminum sp. B
*Justicia microcarpa
*Justicia robinsonii
*Justicia rupestris
*Justicia subalternans
Justicia valida
*Kopsia griffithii var. paucinervia
*Lagerstroemia langkawiensis
*Lasiobema flavum
Leptopus australis
Leucas mollissima
Ligustrum confusum
Lysimachia peduncularis
*Madhuca calcicola
*Mallotus bracteatus
Mallotus brevipetiolatus
Mallotus cuneatus
Maytenus curtisii
*Melodinus perakensis
Microphium pubescens
*Miliusa parviflora
*Millettia pterocarpa
Monophyllaea glabra
*Monophyllaea hirticalyx
Oldenlandia rosettifolia
*Ophiorrhiza fruticosa
Ophiorrhiza kunstleri
*Ophiorrhiza longerepens
Ornithoboea flexuosa
Orophea cuneiformis
*Orophea hirsuta
Orophea polycarpa
*Osmanthus scortechinii
*Paraboea bakeri
*Paraboea bettiana
*Paraboea ferruginea
*Paraboea laxa
*Paraboea vulpina
Parishia rosea
*Pavetta pauciflora
Pentacme siamensis
Pentaspadon curtisii
Peperomia dindigulensis
Peperomia portulacoides
*Peperomia sp. A.
*Phanera decumbens
Phyllanthus columnaris
Phyllanthus ridleyanus
*Pilea fruticosa
*Piper collinum
Pisonia aculeata
Pisonia umbellifera
*Pistacia malayana
*Plectranthus kunstleri
Polygala cardiocarpa
Polygala malesiana
Polygala triphylla
*Polytrema cupreum
*Popowia velutina
*Rungia minutiflora
Sageretia thea
Sapium insigne
*Sauropus calcareus
Sauropus macranthus
Sauropus suberosus
*Schefflera subracemosa
Scleropyrum wallichianum
*Scolopia steenisiana
Semecarpus glomerulata
Solanum biflorum
*Sonerila elliptica
Sonerila tenera
*Stenothyrsus ridleyi
Stephania venosa
Sterculia angustifolia
Sterculia lancaviensis
*Strobilanthes pachyphyllus
Tarenna angustifolia
*Tarenna calcarea
Tarenna curtisii
Tetrameles nudiflora
Timonius atropurpureus
*Toxocarpus pauciflorus
Trigonostemon verticillatus
*Tylophora calcicola
Vernonia curtisii
*Vernonia rupicola
Vitex siamica
*Vitis scortechinii
Wikstroemia androsaemifolia
*Zanonia clarkei
*Zizyphus pernettyoides

MONOCOTYLEDONS

*Aglaonema costatum
Amorphophallus carnosus
Amorphophallus haematospadix
Arisaema fimbriatum
Arthraxon prionodes
Asparagus racemosus
*Boesenbergia curtisii
*Calamus balingensis
Calanthe rubens
Calanthe vestita
*Carex malaccensis
Carex speciosa
*Corymborchis brevistylis
Cymbopogon calcicola
*Dendrobium langkawiense
Dendrocalamus dumosus
*Dendrocalamus elegans
Dichanthium annulatum
*Dichanthium mucronulatum
Dracaena curtisii
Dracaena yuccaefolia
Eulalia quadrinervis
Eulophia keithii
*Fimbristylis calcicola
*Fimbristylis malayana
*Fimbristylis trichophylla
*Globba albiflora var. aurea
Goodyera hispida
Habenaria carnea
*Habenaria kingii
Hapaline brownii
*Isachne langkawiensis
Kaempferia elegans
Kaempferia pulchra
*Liberbaileya gracilis
*Malaxis reniloba
*Malleola undulata
*Maxburretia rupicola
*Oberonia calcicola
Oberonia caudata
*Oberonia transversiloba
*Pandanus calcicola
*Pandanus irregularis
*Pandanus piniformis
Paphiopedilum niveum
Pollia subumbellata
Pomatocalpa naevatum
Pomatocalpa setulense
*Pothos lorispatha
*Pteroceras tanyphyllum
*Raphidophora kunstleri
Sarcanthus termissus
Spathoglottis hardingiana
*Stachyphrynium cylindricum
*Thelasis succosa
Trichoglottis winkleri var. minor
*Typhonium filiforme
*Typhonium fultum

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*Endemic to Malaya.

II. PREFERENTS

PTERODOPHYTES

Adiantum malesianum
Adiantum soboliferum
Asplenium adiantoides
Asplenium squamulatum
Cyclopeltis crenata
Hemionitis arifolia
Pteridrys syrmatica
*Pteris longipinnula var. b
Pyrrosia penangiana

GYMNOSPERMS

ANGIOSPERMS

DICOTYLEDONS

*Argostemma inaequilaterum
Argostemma pictum
Berrya cordifolia
Chirita viola
Cladogynos orientalis
Cleistanthus gracilis
*Cleistanthus kingii
Colona merguensis
Croton cascarilloides
Cymaria dichotoma
*Debregeasia squamata
Deeringia polysperma
*Dehaasia curtisii
Desmodium rugosum
*Drypetes oxyodonta
Epithema saxatile
Fagraea carnosa
Fagraea curtisii
Ficus curtipes
Garcinia minutiflora
Gomphostemma crinitum
Hedyotis coronaria
*Heterostemma piperifolium
Hopea ferrea
*Hoya citrina
Illigera pulchra
*Ixora clerodendron
Jasminum wrayi
*Justicia henicophylla
Lasiobema curtisii
*Lasiobema strychnoideum
*Leea saxatilis
Litsea glutinosa
*Madhuca ridleyi
Mallotus dispar
Mallotus miquelianus
Memecylon laevigatum
*Miliusa amplexicaulis
Monophyllaea horsfieldii
Murraya paniculata
*Orophea maculata
*Paraboea capitata
*Peperomia kotana
*Phyllanthus filicifolius
Procris pedunculata
Rinorea bengalensis
Sauropus villosus
Sumbaviopsis albicans
Terminalia triptera
Trigonostemon viridissimus
Vitis discolor
Wikstroemia indica
Zizyphus oenoplia

MONOCOTYLEDONS

Abdominea minimiflora
Amomum testaceum
Apluda mutica
Appendicula torta
Arachnis flos-aeris
Bulbophyllum fenestratum
*Bulbophyllum flammuliferum
Bulbophyllum lilacinum
Dendrobium salaccense
Dioscorea calcicola
Dracaena congesta
*Dracaena graminifolia
*Globba fasciata
Habenaria reflexa
Pholidota pallida
*Pothos macrocephalus
*Sarcanthus rugulosus
Trichoglottis retusa
Uncifera tenuicaulis

III. INDIFFERENTS

PTERIDOPHYTES

Adiantum stenochlamys
Asplenium macrophyllum
Asplenium pellucidum
Asplenium salignum
Davallia denticulata
Davallia solida
Drynaria quercifolia
Drynaria rigidula
Humata pectinata
Loxogramme avenia
Loxogramme scolopendrina
Nephrolepis falcata
Photinopteris speciosa
Phymatodes nigrescens
Phymatodes papillosum
Phymatodes scolopendria
Pityrogramma calomelanos
Pteridium aquilinum var. wightianum
Pteridium caudatum var. yarrabense
Pteris ensiformis
Pteris tripartita
Pteris vittata
Pyrrosia adnascens
Pyrrosia varia
Tectaria variolosum
Thelypteris immersa
Trichomanes bipunctatum

GYMNOSPERMS

Cycas rumphii
Podocarpus polstachyus

ANGIOSPERMS

DICOTYLEDONS

Actephila ovalis
Adenia nicobarica
Aeschynanthus parvifolia
*Aglaia argentea
Aglaia odoratissima
Aglaia splendens
Agrostistachys gaudichaudii
Allophylus cobbe var. glaber
Allophylus cobbe var. villosus
Alyxia selangorica
Antidesma japonicum
*Ardisia fulva
*Ardisia kunstleri
Ardisia lancelolata
Ardisia oxyphylla
*Ardisia solanacea var. elata
*Ardisia vaughani
Argyreia maingayi
Argyreia mollis
*Artabotrys grandifolius
Atalantia monophylla
*Atalantia roxburghiana
Becheria parviflora
*Begonia debilis
Begonia guttata
*Beilschmiedia lumutensis
Bombax anceps
Bridelia ovata
Bridelia tomentosa
Callicarpa lanata
Canthium didymum
Carallia brachiata
Casearia capitellata
Cassia timoriensis
Cinnamomum iners
Clausena excavata
*Cleidion javanicum
Cleistanthus decurrens
*Cleistanthus glaucus
*Cleistanthus macrophyllus
Clerodendron penduliflorum
Clerodendron serratum
Clidemia hirta
Combretum porterianum
Congea vestita
Connarus sp.
Cordia griffithii
Cordia obliqua
Cratoxylum maingayi
Cyclea laxiflora
*Dalbergia kunstleri
Dalbergia phyllanthoides
Dalbergia scortechinii

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*Endemic to Malaya.

Dicotyledons (cont.)

Decaspermum fruticosum
*Dehaasia longipedicellata
Dendrocnide stimulans
Desmos cochinchinensis
Desmos dasymaschalus var. wallichii
Desmos dunalii
*Diospyros adenophora
Diospyros buxifolia
Diospyros cauliflora
*Diospyros ellipsoidea
Diospyros ferrea
Diospyros frutescens
Diospyros toposiodes
Dischidia benghalensis
Dischidia hirsuta
*Dischidia scortechinii
Ehretia timorensis
*Elatostema curtisii
Elatostema latifolium
*Enicosanthum congregatum
Eriobotrya bengalensis
Erismanthus obliquus
*Ervatamia peduncularis
Erythroxylum cuneatum
*Eugenia pendens
*Eugenia porphyranthera
Euonymus cochinchinensis
Fagraea blumei
Ficus binnendykii
Ficus deltoidea
Ficus elastica
Ficus hispida
Ficus microcarpa
Ficus sagittata
Ficus subulata
Ficus sundaica
Ficus superba var. japonica
Ficus tinctoria ssp. gibbosa
Ficus virens var. glabella
Ficus villosa
Garcinia murdochii
Garcinia nigrolineata
*Garcinia opaca
Geophila repens
Glochidion rubrum
Glycosmis puberula
Glycosmis rupestris
*Glycomis sapindoides
Glytopetalum quadrangulare
Gomphia serrata
Gomphostemma javanicum
Gomphostemma microcalyx
*Goniothalamus fulvus
Grewia acuminata
*Gymnostachyum decurrens
*Gymnostachyum diversifolium
Hedvotis tenelliflora
Hedyotis verticillata
Helicteres angustifolia
Helicteres hirsuta
Helixanthera axillaris
Helixanthera pulchra
Hemigraphis ridleyi
Heritiera littoralis
Holarrhena curtisii
Homalanthus populneus
Homalium dasyanthum
Hoya coronaria
Hoya latifolia
*Hoya maingayi
Hoya parviflora
Hoya ridleyi
Hydnocarpus wrayi
Iodes cirrhosa
Iodes ovalis
Ipomoea illustris
Ixora nigricans var. ovalis
Ixora pendula
Ixora umbellatta var. multibracteata
Jacquemontia paniculata
Jasminum adenophyllum
Jasminum insularum
*Justicia pectinella
*Justicia ptychostoma
*Justicia subcymosa
*Justicia uber
Knema globularia
Knema laurina
Kopsia pauciflora
Laportea interrupta
Leea aequata
Leea rubra
Leea sambucina
Leptonychia glabra
Ligustrum robustum
Litsea norohae
Loeseneriella pauciflora
Macaranga tanarius
Macrosolen cochinchinensis
*Maesa pahangiana
Malaisia scandens
Mallotus wrayi
Mammea brevipes
Marsdenia tinctoria
*Medinilla scortechinii
Meiogyne virgata
Melochia umbellata
*Melodinus orientalis
Melothria affinis
*Memecylon dichotomum
Memecylon edule
Memecylon floribundum
*Memecylon kunstleri
Memecylon pauciflorum
*Memecylon wallichii
Microdesmis casearifolia
Micromelum minutum
Milusa longipes
Mimusops elengi
Momordica subangulata
Morinda elliptica
Morinda umbellata
Mucuna biplicata
Mycetia malayana
Myrsine porteriana
Naravelia dasyoneura
Neolitsea zeylanica
Oldenlandia ovatifolia
Oldenlandia pterita
Ophiorrhiza discolor
Ophiorrhiza hispidula
*Ophiorrhiza pallidula
Ophiorrhiza remotiflora
Orophea enterocarpa
Orthosiphon aristatus
Oxymitra biglandulosa
Pachycentria constricta
Paederia tomentosa
Paramignya scandens
Paranephelium macrophyllum
Payena lucida
Petunga hirta
Phanera glauca
Phyllanthus oxyphyllus
Phyllanthus pulcher
Phyllanthus sikkimensis
*Piper mucronatum
*Piper scortechinii
Piper umbellatum
Planchonella obovata
*Plethiandra sessiliflora
Pogonanthera pulverulenta
Poikilospermum suaveolens
*Polyalthia brunneifolia
*Polyalthia lateritia
Polytrema uber
*Prema rubens
Prismatomeris malayana
Pseuderanthemum crenulatum
Pseuderanthemum graciliflorum
Pseuduvaria macrophylla
Pseuduvaria setosa
Psychotria angulata
*Psychotria cantleyi
Psychotria montana
Psychotria rhinocerotis
Pterolobium densiflorum
Pterospermum jackianum
Pterospermum pectiniforme
*Quisqualis parvifolia
Radermachera lobbii
Randia densiflora
Rauwolfia reflexa
*Richeriella malayana
Rinorea horneri
Rostellaria procumbens
*Rubus angulosus
Ruellia repens
*Rhus perakensis
Salacia grandiflora
Salacia korthalsiana
Salacia macrophylla
Salomonia ciliata
Saraca declinata
Saraca thaipingensis
Secamone micrantha
Schefflera junghuhniana
*Schefflera musangensis
Schefflera subulata
Schefflera tomentosa
Schefflera venolusa
Scolopia spinosa
Scurrula ferruginea
Scutellaria discolor var. discolor

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Dicotyledons (cont.)

Sida javensis
Stauranthera grandifolia
Stelechocarpus cauliflorus
Sterculia rubiginosa
Streblus asper
Streblus ilicifolius
Streblus taxoides
*Strobilanthes leucopogon
Strychnos axillaris
*Tarenna pulchra
*Tarenna ridleyi
Terminalia calamansanai
*Toxocarpus curtisi
Trema tomentosa
Trigonostemon aurantiacus
Trichosanthes tricuspidata
*Trigonostemon villosus
*Tristania subauriculata
Trivalvaria macrophylla
Turpinia ovalifolia
Tylophora perakensis
Tylophora tenuis
Vaccinium littoreum
Vatica cinerea
Ventilago gladiata
Ventilago oblongifolia
Villebrunea sylvatica
Viscum orientale
Vitis furcata
Vitis glaberrima
Vitis hastata
*Vitis kunstleri
*Vitis mollissima
Vitis pyrrhodasys
Vitis repens
*Vitis wrayi
Wrightia dubia
Wrightia laevis

MONOCOTYLEDONS

*Adenoncos major
Adenoncos parviflora
Adenoncos sumatrana
Aglaonema oblongifolium
Agrostophyllum bicuspidatum
Alocasia denudata
Alocasia lowii
Amorphophallus prainii
Amorphophallus variabilis
Amydrium humile
Anadendrum marginatum
*Arenga hookeriana
*Arenga westerhoutii
Arisaema roxburghii
Borassodendron machadonis
Bulbophyllum apodum
Bulbophyllum concinnum
Bulbophyllum membranaceum
Burmannia championii
Burmannia lutescens
Calamus concinnus
Calamus siamensis var. malaianus
Calanthe ceciliae
Calanthe triplicata
Camarotis apiculata
Carex breviscapa
Caryota mitis
Catimbium speciosum
Centhotheca lappacea
Ceratostylis pendula
Chlorophytum orchidastrum
Chrysopogon fulvus
Chrysopogon orientalis
Coelogyne asperata
*Coelogyne pallens
Coelogyne pandurata
Colocasia gigantea
Corybas mucronatus
Corymborchis veratrifolia
Cymbidium finlaysonianum
Dendrobium aloifolium
Dendrobium spurium
Dichanthium caricosum
Dioscorea bulbifera
Dioscorea esculenta
Dioscorea filiformis
Dioscorea glabra
Dioscorea prazeri
Dracaena angustifolia
*Dracaena nutans
Ephemerantha luxurians
Epipremnum giganteum
Eria leptocarpa
Eria pulchella
Fimbristylis fusca
Fimbristylis fuscoides
*Forrestia monosperma
Hanguana malayana
*Homalomena deltoidea
*Iguanura polymorpha
Lasia aculeata
Liparis caespitosa
Liparis gibbosa
Malaxis calophylla
Malleola dentifera
Microsaccus ampullaceus
Microsaccus brevifolius
Microsaccus javensis
Neyraudia reynaudiana
*Oberonia flava
Oplismenus compositus
*Pandanus alticola
*Peliosanthes lurida
Phalaenopsis cornu-cervi
Phalaenopsis decumbens
Phreatia secunda
Podochilus lucescens
Podochilus microphyllus
Pogonatherum paniceum
Pollia sumatrana
Polystachya flavescens
Pomatocalpa spicatum
Pothos scandens
Pteroceras ciliatum
Pteroceras hirsutum
Renanthera histrionica
Rhychelytrum repens
Sarcanthus sacculatus
Sarcanthus scortechinii
Sarcanthus subulatus
Schismatoglottis calyptrata
*Schismatoglottis mutata
*Sciaphila asterias
Scindapsus hederaceus
Scindapsus perakensis
Scleria lithosperma
Stemona tuberosa
Thelasis micrantha
Thelasis triptera
*Tupistra grandis
Vandopsis gigantea

IV. STRANGERS

PTERIDOPHYTES

Abacopteris urophylla
Antrophyum callifolium
Antrophyum semicostatum
Arcypteris irregularis
Asplenium phyllitidis
Asplenium unilaterale
Athyrium cordifolium
Athyrium esculentum
Athyrium montanum
Athyrium pinnatum
*Athyrium prescottianum
Blechnum finlaysonianum
Crypsinus enervis
Ctenopteris alata
Ctenopteris moultoni
Cyclosorus extensus
Cyclosorus interruptus
Cyclosorus megaphyllus
Cyclosorus unitus
Drynaria sparsisora
Humata heterophylla
Lemmaphyllum accedens
Lepisorus longifolius
Leptochilus decurrens
Lindsaya lucida
Lygodium flexuosum
Microlepia speluncae
Microsorium musifolium
Microsorium punctatum

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Pteridophytes (*cont.*)

Nephrolepis biserrata
Nephrolepis hirsutula
Nephrolepis radicans
Oleandra undulata
Pteris mertensioides
*Pteris scabripes
Pyrrosia floccigera
Taenitis blechnoides
Tectaria barberi
Tectaria griffithii
Tectaria macronta
Trichomanes christii
Trichomanes humile
Trichomanes motleyi
Vittaria angustifolia
Vittaria elongata var. angustifolia

GYMNOSPERMS

Agathis dammara
Gnetum cuspidatum
Gnetum gnemon var. tenerum
Podocarpus neriifolius

ANGIOSPERMS

DICOTYLEDONS

Acrotrema costatum
Adenosma capitatum
Aeschynanthus radicans
Agelaea borneensis
Alchornea rugosa
Alsomitra pubigera
Alstonia scholaris
*Alyxia angustifolia
*Alyxia pumila
Anaxagorea javanica
Antidesma montanum
Antidesma tomentosum
*Aporosa stellifera
Aralidium pinnatifidum
Ardisia andamanica
Ardisia crenata
Ardisia colorata var. complanata
Ardisia pendula
*Ardisia playtyclada
Ardisia ridleyi
*Ardisia tahanica
Ardisia villosa
Azadirachta excelsa
Baccaurea lanceolata
Balanophora fungosa
Barleria prionitis
Barringtonia asiatica
*Barringtonia fusiformis
Barringtonia macrostachya
Bauhinia acuminata
*Beilschmiedia pahangensis
Biophytum adiantoides
Blumeodendron kurzii
Brassaiopsis polyacantha
Breynia vitis-idaea
Bridelia stipularis
Buchanania sessilifolia
Caesalpinia crista
Calophyllum curtisii
Cananga odorata
Canarium pilosum
Canarium pseudodecumanum
Capparis pubiflora
Cardiopteris javanica
Casearia grewiaefolia
Centranthera hispida
Chloranthus elatior
Chukrassia tabularis
Citrus macroptera
Claoxylon longifolium
Cleistanthus hirsutulus
Cleistanthus polyphyllus
Clerodendron paniculatum
Cnesmone javanica
Coffea canephora
*Coffea malayana
Coleus scutellarioides
Colubrina asiatica
Combretum latifolium
Connarus semidecandrus
Cotylelobium malayanum
Croton argyratus
Croton erythrostachys
Croton laevifolius
Cryptocarya griffithiana
Curanga amara
Cynometra malaccensis
*Cyrtandra cupulata
*Cyrtandra lanceolata
*Dacryodes kingii
Dehassia microcarpa
Derris elliptica
Derris thyrsiflora
Desmodium umbellatum
Dillenia indica
Diospyros hermaphroditica
Diospyros malayana
Diospyros pilosanthera
Diospyros rigida
Diospyros wallichii
Diploclisia glaucescens
Dipterocarpus oblongifolius
Dischidia rafflesiana
Distylium stellare
Dryobalanops aromatica
Dryobalanops oblongifolia
Dysoxylum arborescens
Elaeocarpus pedunculatus
Endospermum diadenum
Erythrina variegata
Eugenia chlorantha
Eugenia claviflora
Eugenia spicata
Euonymus javanicus
Exacum tetragonum
Fagraea auriculata
Fagraea ceilanica
Ficus annulata
Ficus botryocarpa
Ficus montana
Ficus oligodon
Ficus parietalis
Ficus racemosa
Ficus scortechinii
Ficus semicordata
Ficus stricta
Ficus trichocarpa var. obtusa
Firmiana malayana
Garcinia cowa
*Garcinia eugeniaefolia
Garcinia merguensis
*Garcinia montana
Glochidion obscurum
Glochidion perakense
Glycosmis chlorosperma
Gmelina asiatica
Gmelina villosa
Gomphandra quadrifida var. quadrifida
Gomphostemma curtisii
Goniothalamus scortechinii
Goniothalmus uvarioides
Grewia paniculata
Guettarda speciosa
Gymnopetalum cochinchinense
Hedyotis congesta
Homonoia riparia
Hopea dryobalanoides
Horsfieldia tomentosa
*Hoya revoluta
Hunteria zeylanica
Hydnocarpus castanea
Hydnocarpus woodii
Hydnophytum formicarum
Hygrophila angustifolia
Hypserpa cuspidata
*Ilex maingayi
Ixora brunonis
Ixora congesta
Ixora grandifolia
Ixora lobbii var. stenophylla
Ixora nigricans
*Ixora scortechinii
Jasminum bifarium
Justicia vasculosa
Kibara chartacea
Knema cinerea var. patentinervia
Knema cinerea var. rubens
Knoxia corymbosa
Koiledepas longifolium
*Kopsia macrophylla
Lantana camara var. aculeata
Lasianthus stipularis
Lepistemon binectariferum
Leucaena leucocephala
Leucas zeylanica
*Lindera concinna
Lithocarpus elegans
Lithocarpus urceolaris
Litsea polyantha
Ludwigia hyssopifolia
Luvunga eleutherandra
Maesa striata
Mallotus eriocarpus
*Mallotus griffithianus
Mallotus oblongifolius
Mallotus peltatus
Mallotus philippensis
Mallotus repandus

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*Endemic to Malaya.

Dicotyledons (*cont.*)

Medinilla crassifolia var. hasseltii
Melaleuca cajuputi
Melanolepis multiglandulosa
Melastoma polyanthum
*Memecylon acuminatum
Memecylon oleaefolium
Mesua ferrea
Millettia hemsleyana
Millettia sericea
*Mitrephora maingayi
Moghania strobilifera
Naravelia laurifolia
Nauclea junghuhnii
Neesia synandra
Neonauclea calycina
Nepenthes sp.
Ophiorrhiza communis
Palaquium obovatum
Palaquium ottolanderi
Parameria polyneura
Parashorea lucida
Pavetta indica
Pavetta naucleiflora
Peltophorum pterocarpum
Phanera integrifolia
Phoebe lanceolata
Piper boehmeriaefolium
Piper caninum
*Piper porphyrophyllum
Piper retrofractum
Pittosporum ferrugineum
Polyalthia cauliflora var. beccarii
Polyalthia cinnamomea
*Polyalthia hypogaea
Polyalthia motleyana var. glabrescens
Polyalthia rumphii
Polyalthia stenopetala
Polygonum chinense
Premna pyramidata
Psychotria rostrata
Psychotria sarmentosa
Psychotria viridiflora
Pterygota alata
Pterisanthes coriacea
Rauvolfia perakensis
Reissantia indica
Rhododendron longiflorum var. longiflorum
Rhynchoglossum obliquum
Rinorea anguifera
Rinorea macrophylla
Sageraea elliptica
Sauropus brevipes
*Schefflera elegans
Shorea guiso
Shorea leprosula
Shorea ovalis
Solanum decemdentatum
Spondias dulcis
Stauranthera umbrosa
Streblus laxiflorus
Tamarindus indica
*Tarenna appressa
Tetracera scandens
Thespesia populnea
Thunbergia fragans var. javanica
Tinomiscium petiolare
Tinospora crispa
Trema orientalis
Tristania merguensis
*Turraea breviflora
Urophyllum corymbosum
Urophyllum glabrum
Utricularia minutissima
Uvaria cordata
Uvaria javana
Viburnum sambucinum
Vitex pubescens
Vitis lanceolaria
Vitis martinelli
Vitis novemfolia
Vitis peduncularis
Wikstroemia polyantha
Xanthophyllum glaucum
*Xerospermum wallichii
Xylocarpus granatum
Xylopia malayana
Zippelia begoniaefolia

MONOCOTYLEDONS

Acampe longifolia
*Achasma macrocheilos
Achasma megalocheilos
Achasma triorgyale
Aerides odoratum
Agrostophyllum hasseltii
Agrostophyllum majus
*Amomum biflorum
*Anadendrum latifolium
Anadendrum montanum
Aneilema nudiflorum
Appendicula anceps
Appendicula cornuta
Appendicula undulata
Areca triandra
Arenga pinnata
Ascochilopsis myosurus
Bulbophyllum pulchellum
Bulbophyllum sessile
*Calamus ornatus var. horridus
Carex perakensis
Coelogyne rochussenii
*Corymborchis rhytidocarpa
Costus globosus
Costus speciosus
Crinum defixum
*Cryptocoryne affinis
*Cryptocoryne minima
*Cryptocoryne purpurea
Curculigo latifolia
Cymbidium dayanum
Cyperus trialatus
Cyrtosperma lasioides
Dendrobium acerosum
Dendrobium excavatum
Dendrobium farmeri
Dendrobium indivisum
Dendrobium leonis
Dendrobium planibulbe
Dendrobium pumilum
Dendrobium secundum
Dendrobium subulatum
*Dendrobium tetrodon
Dioscorea hispida
Dioscorea polyclades
Dioscorea prainiana
Dioscorea pyrifolia
Dipodium pictum
Donax grandis
*Dracaena porteri
Ephemerantha fimbriata
Epipremnopsis media
Eria citrina
Eria leiophylla
Eria nutans
Eria pannea
Eria vestita
Eurycles sylvestris
Geodorum citrinum
Globba patens
Gymnosiphon aphyllus
Hippeophylum scortechinii
Homalomena griffithii
Homalomena humilis
Homalomena rubra
Iguanura geonomaeformis
Ischaemum indicum
Ischaemum timorense
Leptaspis urceolata
*Licuala modesta
Liparis compressa
Livistona saribus
Malaxis latifolia
Malaxis micrantha
Musa malaccensis
Oberonia anceps
Oberonia dissitiflora
Oberonia spathulata
Onchosperma horridum
*Orchidantha longiflora
Pandanus odoratissimus
Pandanus recurvatus
Panicum sarmentosum
Paphiopedilum lowii
Paspalum conjugatum
Peliosanthes violacea
*Phaeomeria maingayi
Plectocomia griffithii
Poaephyllum pauciflorum
Podochilus tenuis
Pollia sorzogonensis
Pollia thyrsiflora
Polytrias amaura
Pomatocalpa kunstleri
Pomatocalpa latifolium
*Pothos latifolius

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*Endemic to Malaya.

Monocotyledons (*cont.*)

Raphidophora beccarii
Raphidophora korthalsii
*Raphidophora maingayi
Renanthera elongata
Sarcanthus machadonis
Schoenorchis micrantha
Scindapsus scortechinii
Scleria purpurascens
Setaria palmifolia
Staurochilus fasciatus
Stenotaphrum helferi
Tacca leontopetaloides
Taeniopyllum culciferum
Taeniophyllum filiforme
Taeniophyllum obtusum
Thecostete alata
Thelasis carinata
Thrixspermum album
Thrixspermum amplexicaulis
Thysanolaena maxima
Trichoglottis misera
Tropidia curculigoides
*Zingiber spectabile

WEEDS AND ESCAPES

PTERIDOPHYTES

Adiantum tenerum

GYMNOSPERMS

—

ANGIOSPERMS

DICOTYLEDONS

Abutilon indicum ssp. indicum
Acalypha lanceolata
Ageratum conyzoides
Aleurites moluccana
Bidens pilosa
Boehmeria nivea
Cyathula prostrata
Erechtites valerianifolia
Eupatorium odoratum
Euphorbia hirta
Flacourtia jangomas
Hyptis rhomboidea
Hyptis suaveolens
Mikania cordata
Mimosa pudica
Muntingia calabura
Murraya koenigii
Passiflora foetida var. hispida
Physalis minima
Pilea microphylla
Piper nigrum
Scoparia dulcis
Solanum ferox
Solanum nigrum
Solanum torvum
Spondias pinnata
Tridax procumbens
Urena lobata
Vernonia cinerea

MONOCOTYLEDONS

Axonopus compressus
Chrysopogon aciculatus
Coix lacryma-jobi
Colocasia antiquorum
Cyperus kyllingia
Digitaria violascens
Eleusine indica
Imperata cylindrica var. major
Rhoeo spathacea

TABLE 3. AFFINITIES OF THE FLORISTIC COMPONENTS
NUMBER OF SPECIES

	Pterido-phytes	Gymno-sperms	Dicoty-ledons	Monocoty-ledons	Total	%
EXCLUSIVES	15	1	182	62	257	21.1
PREFERENTS	9	—	53	19	81	6.6
INDIFFERENTS	27	2	285	104	415	34.1
STRANGERS	45	3	257	131	424	34.9
WEEDS AND ESCAPES	1	—	29	9	39	3.2

The species known in Malaya only from limestone (exclusives, which includes endemic and non-endemics) total 257. This is an increase of 62 over Henderson's (1939) figure of 195. However the percentage which is 21.1% of the present total is less than Henderson's figure of 26% of his total. This is because of the even greater increase in the overall total (from 745 to 1216) of the species recorded from the limestone. The total number of species endemic and restricted to the limestone remains unchanged with no new additions. Henderson recorded about 130 species, the present figure is exactly 129 species.

The characteristic species of the limestone which are the exclusives and preferents number 338. This is 27.7% of the total flora. The indifferents and strangers are represented by 839 species (69.0% of the total flora), forming the bulk of the flora. The weeds and escapes are poorly represented by only 39 species (3.2% of the total flora).

SECTION II — The Flora

PTERIDOPHYTES

INTRODUCTORY KEY TO THE FERNS

The numbers on the right hand side refer to the numbers in the main key with which one should continue.

1\. Fronds of two distinct forms; nest and foliage .... 2. *Drynaria* spp.
1\. Fronds not as above.
  2\. Filmy ferns; laminar part of fronds one cell thick ....6. *Trichomanes* spp.
  2\. Not filmy ferns; fronds thicker, usually several cells thick.
    3\. Fronds twining .... 11. *Lygodium* spp.
    3\. Fronds not twining.
      4\. Fronds simple, erect, grass-like .... 12. *Schizaea inopinata*
      4\. Fronds not as above.
        5\. Fronds simple, entire or lobed.
          6\. Fronds entire.
            7\. Base of fronds cordate or sagittate, stipitate. .... 16 *Athyrium cordifolium, Hemionitis arifolia, Doryopteris* spp.
            7\. Base of fronds simple, if cordate then sessile.
              8\. Stipe articulated .... 19. *Oleandra undulata*
              8\. Stipe if present, not articulated.
                9\. Sori marginal or sub-marginal .... 20. *Vittaria* spp.
                9\. Sori not marginal or sub-marginal.
                  10\. Sori indusiate .... 23. *Humata heterophylla, Asplenium* spp. (some)
                  10\. Sori non-indusiate.
                    11\. Sori acrostichoid .... 26.
                    11\. Sori not acrostichoid.
                      12\. Sori elongate along veins .... 28. *Loxogramme* spp., *Antrophyum* spp.
                      12\. Sori not elongate.
                        13\. Frond pubescent with stellate hairs .... 3. *Pyrosia* spp.
                        13\. Frond not so pubescent .... 39. *Lemmaphyllum accedens, Lepisorus longifolius, Microsorium* spp. *Crypsinus enervis.*

6. Fronds lobed to more than half way to rachis.

14. Sori only at the end of lobes .... 43.
Ctenopteris alata

14. Sori differently arranged.

15. Sori indusiate .... 45.
Humata pectinata, Doryopteris spp.

15. Sori non-indusiate .... 47.
Polypodium papillosum, Phymatodes spp.

5. Fronds compound, pinnate or more divided.

16. Undersurface of fronds chalky-white .... 50.
Cheilanthes farinosa, Pityrogramma calomelanos

16. Not so.

17. Sori acrostichoid or sub-acrostichoid .... 52.
Photinopteris speciosa, Heterogonium spp.

17. Sori differently arranged.

18. Sori marginal or sub-marginal, elongate ... 55.
Lindsaya lucida, Pteridium spp., *Pteris* spp.

18. Sori not marginal or sub-marginal, if marginal or sub-marginal, then not elongate.

19. Sori marginal or sub-marginal.

20. Sori on reflexed marginal flaps .... 65. *Adiantum* spp.

20. Sori otherwise.

21. Fronds simply pinnate ...... 70.
Ctenopteris moultoni, Nephrolepis spp. (some)

21. Fronds more divided ...... 73.

19. Sori not marginal or sub-marginal.

22. Sori elongate .... 75.
Taenitis blechnoides, Blechnum finlaysonianum, Athyrium spp., *Asplenium* spp. (some)

22. Sori rounded.

23. Sori indusiate.

24. Fronds pinnate or bipinnatifid .... 86.
Polystichum lindsaefolium, Pteridrys syrmatica, Cyclopeltis crenata, Nephrolepis spp. (some), *Thelypteris immersa, Cyclosorus* spp.

24. Fronds bipinnate or more amply divided .... 95.
Tectaria spp., *Microlepia speluncae*

23. Sori non-indusiate .... 101.
Abacopteris urophylla, Acrypteris irregularis

FERNS — MAIN KEY

1. Fronds of two distinct forms, nest and foliage leaves 2
Fronds not differentiated into nest and foliage leaves 5

2. Nest leaves lobed 2 cm or more deep 3
Nest leaves not or only very shallowly scalloped .... *Drynaria bonii*

3. Foliage leaves pinnate; pinnae stalked .... *Drynaria rigidula*
Foliage leaves lobed 4

4. Rhizome covered by short appressed scales. Sori in two irregular rows .... *Drynaria sparsisora*
Rhizome covered by long, semi-erect scales. Sori in two regular rows .... *Drynaria quercifolia*

5. Sori enclosed by the hollow base of indusium. Sporangia on an elongate receptacle. Filmy ferns 6
Sori different. Not filmy ferns 10

6. Rhizome erect; fronds tufted .... *Trichomanes obscurum*
Rhizome creeping; fronds borne at intervals 7

7. Fronds simple, orbicular to broadly ovate .... *Trichomanes motleyi*
Fronds pinnate or more dissected 8

8. Fronds with false veins 9
Fronds with no false veins .... *Trichomanes humile*

9. Soral-lips of two triangular lobes .... *Trichomanes bipunctatum*
Soral-lips not lobed, trumpet-like .... *Trichomanes christii*

10. Fronds twining, long climbing 11
Fronds different 12

11. Sterile leaflets regularly lobed; plant of forest shade .... *Lygodium polystachyum*
Sterile leaflets not lobed or only the basal leaflets lobed; usually in partly open places .... *Lygodium flexuosum*

12. Fronds simple, erect, narrow and grass-like .... *Schizaea inopinata*
Fronds different 13

13. Fronds simple, entire or lobed 14
Fronds compound, pinnate or more divided 49

14. Fronds entire or almost entire, base cordate, sagittate, or simple 15
Fronds lobed, usually to more than half-way to rachis 43

15. Frond base cordate or sagittate, stalked 16
Frond base not cordate or sagittate, or if appearing cordate then sessile 19

16. Fronds broadly lanceolate .... *Athrium cordifolium*
Fronds ovate 17

17. Stipes grooved on the adaxial side; sori superficial ... *Hemionitis arifolia*
Stipes not grooved; sori sub-marginal 18

18. Hydathodes present as a series of sub-marginal white spots; marginal veins mostly free .... *Doryopteris ludens*
Hydathodes absent; marginal veins mostly jointed ... *Doryopteris allenae*

19. Stipes articulated at a point between the rhizome and blade ....
.... *Oleandra undulata*
Stipes not articulated 20

20. Sori marginal or sub-marginal 21
Sori not marginal or sub-marginal 22

21. Fronds sessile, 20 by 0.2 – 0.3 cm .... *Vittaria angustifolia.*
Fronds stipitate, to 90 by 0.5 cm ...... *Vittaria elongata* var *angustifolia*

22. Sori indusiate 23
Sori non-indusiate 26

23. Rhizome long creeping; fronds dimorphic .... *Humata heterophylla*
Rhizome short, erect; fronds not dimorphic 24

24. Fronds simple 25
Fronds pinnate .... *Asplenium salignum*

25. Veins of fronds united in a sub-marginal vein ...... *Asplenium phyllitidis*
Veins of frond all free .... *Asplenium squamulatum*

26. Sori acrostichoid or sub-acrostichoid .... *Leptochilus decurrens*
Sori not acrostichoid or sub-acrostichoid 27

27. Sori elongate along veins 28
Sori not elongate along veins 32

28. Sori obique to the midrib, in roughly parallel rows 29
Sori along many veins, forming a network 30

29. Midrib raised on the lower surface, almost flat above ....
.... *Loxogramme scolopendrina*
Midrib raised on the upper surface, almost flat below ....
.... *Loxogramme avenia*

30. Paraphyses in sori club-shaped 31
Paraphyses in sori thread-like .... *Antrophyum callifolium*

31. Stipes to 10 cm; fronds to 30 by 10 cm ...... *Antrophyum semicostatum*
Stipes not distinct; fronds smaller, to 15 by 2 cm ....
.... *Antrophyum parvulum*

32. Fronds densely or sparsely covered by stellate hairs, more on the lower surface 33
Fronds not covered by stellate hairs 39

33. Sterile fronds much longer than broad 34
Sterile fronds orbicular to broadly ovate ...... *Pyrrosia nummularifolia*

34. Sori in a single row on either side of the midrib, to about 0.5 cm across .... *Pyrrosia angustata*
Sori arranged differently, smaller 35

35. Fronds dimorphic; sterile shorter and sometimes wider 36
Fronds not dimorphic; sterile about the same size and shape 37

36. Sterile fronds 1 – 1.5 cm wide; fronds when dried, the margins involuted the upper surface becoming concave; scales of rhizome not closely appressed .... *Pyrrosia adnascens*
Sterile fronds 2 – 3.5 cm wide; fronds when dried, the margins revoluted, the upper surface becoming convex; scales of rhizome not closely appressed .... *Pyrrosia varia*

37. Lower surface of frond densely brown-stellate pubescent .... *Pyrrosia stigmosa*
Lower surface sparsely pubescent, not brown 38

38. Fronds about 1.8 cm wide; sori on the apical half or whole of frond; no clear margin at the edge .... *Pyrrosia floccigera*
Fronds 3 – 6 cm wide; sori on the apical third of frond; with a clear margin to 1 cm wide at the edge .... *Pyrrosia penangiana*

39. Sori in two rows, one on either side of the midrib 40
Sori scattered all over the surface 41

40. Fertile part of frond narrowed; frond less than 15 cm long .... *Lemmaphyllum accedens*
Fertile part of frond not narrowed; frond to over 30 cm long .... *Lepisorus longifolius*

41. Fronds stipitate 42
Fronds sessile, widening abruptly from the base .... *Microsorium musifolium*

42. Stipes 1 cm or less; fronds widening very gradually from the base .... *Microsorium punctatum*
Stipes 5 cm or more; fronds with broad bases .... *Crypsinus enervis*

43. Sori only at the ends of the lobes of frond; usually 2 – 5 on each lobe .... *Ctenopteris alata*
Sori differently arranged 44

44. Sori indusiate 45
Sori non-indusiate 47

45. Sori continuous along margins of fronds 46
Sori not so; in two rows, one on either side of midrib .... *Humata pectinata*

46. Hydathodes present as a series of submarginal white spots; marginal veins mostly free .... *Doryopteris ludens*
Hydathodes not present; marginal veins mostly joined .... *Doryopteris allenae*

47. Veins anastomosing. Rhizome stout, to over 1 cm diameter 48
Veins all free, forked once. Rhizome slender, 0.2 – 0.3 cm diameter .... *Polypodium papillosum*

48. Fronds with 1 – 4 pairs of lobes; sometimes simple .... *Phymatodes scolopendria*
Fronds with 7 – 10 pairs of lobes; never simple .... *Phymatodes nigrescens*

49. Underside of fronds completely or partially covered by chalky-white power 50
Underside of fronds not chalky-white 51

50. Fronds to 20 cm long, often less; sporangia near the margin of frond .... *Cheilanthes farinosa*
Fronds much larger, 30–60 cm long; sporangia scattered all over the undersurface of frond .... *Pityrogramma calomelanos*

51. Sori acrostichoid or sub-acrostichoid, on the apical part of frond or on a special fertile frond 52
Sori not acrostichoid or sub-acrostichoid 54

52. Pinnae entire .... *Photinopteris speciosa*
Pinnae lobed 53

53. Sori indusiate .... *Heterogonium alderwereltii*
Sori exindusiate .... *Heterogonium pinnatum*

54. Sori marginal or submarginal, continuous in a short or long band 55
Sori not marginal or submarginal, if marginal or submarginal, rounded or short, not banded 63

55. Sori short banded, uniting the end of several veins ...... *Lindsaya lucida*
Sori continuous. 56

56. Fronds tripinnate or quadripinnatifid; of long continued growth 57
Fronds pinnate or tripinnatifid or rarely tripartite; not of long continuous growth 58

57. Ultimate segments widely spaced, connected by a wing decurrent from the preceeding segment .... *Pteridium caudatum* var. *yarrabense*
Ultimate segments close together, not connected by a wing .... *Pteridium aquilinum* var. *wightianum*

58. Pinnae all simple, entire .... *Pteris vittata*
Pinnae lobed or branched 59

59. Fronds dimorphic in mode of branching; sterile, with deeply lobed pinnae; fertile, with only the basal pinnae having a single basiscopic lobe .... *Pteris ensiformis*
Fronds not dimorphic 60

60. Pinnae, margin entire or serrulate .... *Pteris scabripes*
Pinnae, deeply lobed. 61

61. Fronds tripartite, basal pinnae almost as large as the terminal one .... *Pteris tripartita*
Fronds not tripartite 62

62. Fronds less than 50 cm long; lowest vein in each pinnae lobe 3–4 times forked .... *Pteris mertensioides*

63. Sori marginal or submarginal 64
Sori not marginal or submarginal 74

64. Sori on small reflexed marginal flaps 65
Sori otherwise 69

65. Fronds simply pinnate 66
Fronds tripinnate or more divided 68

66. Stipes, rachises and stalks of pinnae winged ...... *Adiantum soboliferum*
Stipes, rachises and stalks of pinnae not winged 67

67. Rachis and pinnae hairy; indusial flaps almost circular .... *Adiantum malesianum*
Rachis hairy on the upper surface only; pinnae glabrous; indusial flaps broader than long .... *Adiantum zollingeri*

68. Fronds tripinnate, basal angle of leaflet usually more than a right-angle .... *Adiantum stenochlamys*
Fronds quadripinnate or more divided, basal angle of leaflet usually less than a right-angle .... *Adiantum tenerum*

69. Fronds simply pinnate 70
Fronds tripinnatifid or more divided 73

70. Sori indusiate; fronds 50 cm or more 71
Sori non-indusiate; fronds 10-20 cm .... *Ctenopteris moultoni, Nephrolepis radicans*

71. Apex of pinnae rounded .... *Nephrolepis radicans*
Apex of pinnae pointed 72

72. Pinnae about 5 cm long, strongly falcate .... *Nephrolepis falcata*
Pinnae about 8 cm long, weakly falcate .... *Nephrolepis hirsutula*

73. Fronds tripinnatifid or tripinnate, no false veins; sori longer than broad .... *Davallia solida*
Fronds quadripinnate or more divided, false veins present; sori about as wide as long .... *Davallia denticulata*

74. Sori elongate 75
Sori rounded 84

75. Sori in a longitudinal band halfway between the margin and costa ...... *Taenitis blechnoides*
Sori different 76

76. Sori elongate along and on either side of the midrib .... *Blechnum finlaysonianum*
Sori not elongate along the midrib 77

77. Sori, on one or both sides of vein; transverse section of the upper part of stipe shows vascular strand with two arms (easily seen in fresh material) 78
Sori, all on one side of vein; transverse section of the upper part of stipe shows vascular strand with four arms 81

78. Fronds simply pinnate; pinnae entire or lobed 79
Fronds more amply divided. Large plant, stipe and frond to 2 m long .... *Athyrium esculentum*

79. Rhizome scales entire 80
Rhizome scales toothed .... *Athyrium pinnatum*

80. Lateral veins of pinnae forked once, basiscopic veinlet simple or forked .... *Athyrium montanum*
Lateral veins of pinnae in pinnate groups, each with 3-4 pairs of veinlets .... *Athyrium prescottianum*

81. Rhizome slender, creeping; fronds at interval ...... *Asplenium unilaterale*
Rhizome stout, short creeping; fronds tufted 82

82. Lower pinnae gradually reduced .... *Asplenium pellucidum*
Lower pinnae not reduced 83

83. Pinnae to 7 by 2 cm .... *Asplenium adiantoides*
Pinnae to 15 by 4.5 cm .... *Asplenium macrophyllum*

84. Sori indusiate; indusia sometimes deciduous 85
Sori non-indusiate 101

85. Fronds pinnate or at most bipinnatifid 86
Fronds bipinnate or more amply divided 95

86. Fronds to 3.5 cm wide .... *Polystichum lindsaeifolium*
Fronds broader 87

87. A tooth is present in the sinus between lobes .... *Pteridrys syrmatica*
No tooth in sinuses 88

88. Sori in three irregular rows on either side of the midrib .... *Cyclopeltis crenata*
Sori not so arranged 89

89. Sori arranged on either side of the costa 90
Sori arranged on either side of the costule 91

90. Sori on marginal lobes .... *Nephrolepis dicksonioides*
Sori not on marginal lobes .... *Nephrolepis biserrata*

91\. Veins of the adjacent lobes of pinnae fused to form an excurrent vein in the sinus. If this is not distinct then lobes only two-third to the costae 92
Veins of the adjacent lobes of pinnae not fused, at the most meeting at the sinus. Lobes almost to the costae .... *Thelypteris immersa*

92\. Sori confined to the lobes of the pinnae, not on the lower veins 93
Sori not confined to the lobes of the pinnae, also on the lower veins 94

93\. Pinnae mostly lobed two-third to the costa. Lowest pair of pinnae not reduced .... *Cyclosorus extensus*
Pinnae lobed one-quarter to one-third to the costa. Lowest pair of pinnae often reduced to auricles .... *Cyclosorus interruptus*

94\. Pinnae to 1 cm wide; costae densely pubescent beneath .... *Cyclosorus unitus*
Pinnae to 3 cm wide; costae minutely pubescent below .... *Cyclosorus megaphyllus*

95\. Basiscopic lobe of the lowest pair of pinnae enlarged 96
Not so. Fronds deeply dissected 100

96\. All sori on anastomosing veins .... *Tectaria amplifolia*
All or nearly all sori on free veins 97

97\. Fronds glabrous on the upper surface, or with some hairs near the sinuses 98
Frond pubescent on the upper surface 99

98\. Scales thin, pale brown. Fertile frond contracted .... *Tectaria variolosa*
Scales stiff, dark purple-brown. Fertile frond not contracted .... *Tectaria griffithii*

99\. Veins anastomosing in the costal and costular areoles only (forming a single row of areoles on either side of the costae and costules) .... *Tectaria devexa*
Veins more amply divided .... *Tectaria macrodonta*

100\. Under-surface of lamina glabrous, glabrecent or rarely pubescent .... *Microlepia speluncae*
Under-surface of lamina densely pubescent .... *Microlepia speluncae* var. *villosissima*

101\. Pinnae not lobed, at most crenate or toothed only .... *Abacopteris urophylla*
Pinnae deeply lobed, often pinnate at the base; basiscopic lobe of lowest pinnae enlarged .... *Arcypteris irregularis*

Adiantaceae

Adiantum malesianum Ghatak, Bull. Bot. Surv. Ind. 5 : 73. 1963; Holtt., Fl. Mal. 2 : 638. 1966.

A. caudatum L., Mant. (1771) 308; Holtt., l.c. 599.

Distributed in N.E. India, S. China, Thailand, Indo-China, Sumatra, Sarawak and Philippines. Common on limestone in Malaya but also found on other rock types. A fern of moderately shaded places.

Adiantum soboliferum Wall. apud Hk., Spec. Fil. 2 : 13. 1851; Holtt., Fl. Mal. 2 : 598. 1966.

Distributed throughout the Old World tropics. In Malaya recorded only from the north and usually on limestone.

Adiantum stenochalamys Bak., Ann Bot. 5 : 29. 1891; Holtt., Fl. Mal. 2 : 602. 1966.

A. opacum Copel., Phil. J. Sc. 1, Suppl. 255, t. 3. 1906.

In Malaya, nearly always found on rocks near the sea. Found inland only on rocks along the Tahan river and on limestone along Sungei Betis in Kelantan.

Adiantum tenerum Sw., in Hk. et Bk., Syn. Fil. (1868) 124; v.A.v.R., Mal. Ferns (1908) 330.

A tropical American species now widely cultivated in tropical, subtropical or even temperate countries. Recorded on limestone as escapes from cultivation; on shady hill slopes.

Adiantum zollingeri Mett. ex Kuhn, Ann. Mus. Bot. Lugd. Bat. 4 : 280. 1869; Holtt., Fl. Mal. 2 : 638. 1966.

A. caudatum L. var. *subglabrum* Holtt., l.c. 600.

Distributed in Ceylon, S. India, Thailand and Indochina. In Malaya recorded only from limestone in Kedah and Perlis.

Antrophyum callifolium Bl., Enum. Pl. Jav. (1828) 111; Holtt., Fl. Mal. 2 : 605. 1966.

A common forest fern, epiphytic or on rocks. Recorded from limestone in South Kelantan and Central Pahang.

Antrophyum parvulum Bl. Enum. Pl. Jav. (1828) 110; Holtt., Fl. Mal. 2 : 605. 1966.

Distributed in Java. In Malaya this species is widely distributed and common on limestone, on rocks; with only one record as an epiphyte (Henderson 1939). It has been recorded from limestone in the south in Johore and apparently absent from the vast tract of forest separating the Johore from the northern limestone. It has been collected away from limestone only twice, both on Penang Hill.

Antrophyum semicostatum Bl., Enum. Pl. Jav. (1828) 110; Holtt., Fl. Mal. 2 : 605. 1966.

An epiphytic fern of mountain forest. Recorded from low elevation on limestone probably as epiphytes in Kelantan. Resembles *A. callifolium* but distinguished by the club-shaped paraphyses.

Cheilanthes farinosa (Forsk.) KLf., Enum. Fil. (1824) 202; Holtt., Fl. Mal. 2 : 592. 1966.

Pteris farinosa Frosk., Fl. Aegypt. Arab. (1775) 187.

Aleuritopteris farinosa Fée, Gen. Fil. (1850–52) 153.

Distributed in most tropical and temperate regions with two records from Malaya, both from limestone. One was from Bukit Baling in Kedah and the other from Bukit Chintamani in Pahang the Chintamani specimen was growing in rock crevices from vertical cliffs.

Doryopteris ludens (Wall.) J. Sm., Hist. Fil. (1875) 289; Holtt., Fl. Mal. 2 : 594. 1966.

Pteris ludens Wall. apud Hk., Spec. Fil. 2 : 210. 1858.

Distributed from N. India and S. China southwards through Malesia. Restricted to limestone in Malaya and all collections except two are from Kedah and Perlis; the exceptions are from Gua Batu, Selangor and Batu Kurau, Perak.

Doryopteris allenae Tryon, Contr. Gray Herb. 91 : 91, 97. 1962; Holtt., Fl. Mal. 2 : 638. 1966.

This species is similar to *D. ludens* in appearance. It differs however in having the rhizome short creeping rather than long creeping, the marginal veins in the sterile lamina mostly jointed rather than free and in not having any hydathodes on the upper surface of the fronds.

Endemic to limestone in Malaya, recorded from Perak and Selangor. Usually in shaded localities from rock crevices.

Hemionitis arifolia (Burm.) Moore, Ind. Fil. (1859) 114; Holtt., Fl. Mal. 2 : 596. 1966.

Asplenium arifolium Burm., Fl. Ind. (1768) 213.

Distributed in Ceylon, India, Burma, Indochina, Malesia and the Philippines. In Malaya only from the north, nearly always from limestone.

Pityrogramma calomelanos (L.) Link, Handb. Gew. 3 : 20. 1833; Holtt., Fl. Mal. 2 : 593. 1966.

Acrostichum calomelanos Linn., Sp. Pl. (1753) 1072.

Pantropic, originating in tropical America. Common in Malaya, from the lowlands to 1,300 m. Frequently one of the early colonisers of open ground. Recorded once from the base of limestone.

Taenitis blechnoides (Willd.) Sw., Syn. Fil. (1806) 24, 220; Bedd., Handb. 410, t. 242; Holtt., Fl. Mal. 2 : 586. 1966.

Pteris blechnoides Willd., Phytogr. (1794) 13.

Vittaria angustifolia Bl., Ennum. Pl. Jav. (1828) 199; Holtt., Fl. Mal. 2 : 610. 1966.

Distributed throughout Malesia. In Malaya, Sumatra, Borneo and Java this is a mountain epiphyte at 600–1800 m. On limestone in Malaya this has been collected as a low epiphyte from 20–300 m; recorded from Kedah, Kelantan and Perlis; uncommon.

Vittaria elongata Sw., Syn. Fil. (1806) 302; Holtt., Fl. Mal. 2 : 614. 1966. var. *angustifolia* Holtt., in l.c.

This variety is endemic to Malaya and found only in the North-west and on Pulau Tioman in the South-east. It is both an epiphyte and rock plant and recorded from only one limestone locality as an epiphyte. The typical variety is a common lowland and mountain epiphyte with a paleotropical distribution.

Dennstaedtiaceae

Arcypteris irregularis (Pr.) Holtt., Reinw. 1 : 193. 1951; Fl. Mal. 2 : 538. 1966.

Polypodium irregulare Pr., Rel. Haenk. 1 : 25. 1825.

A common forest species in Malaya. Recorded once from the small limestone outcrop in deep forest in Johore.

Asplenium adiantoides (L.) C. Chr., Ind. Fil. 1905; Holtt., Fl. Mal. 2 : 431. 1966.

Trichomanes adiantoides L., Sp. Pl. (1753) 1098.

Distributed in Burma, Thailand and southwards to Malesia, Australia and Polynesia. Also in Madagascar.

Resembles *A. macrophyllum* Sw. but generally smaller. Intermediates occur but the extreme forms are very different. More field work and cultivation of this species will help to clarify the growth form of this species. Presently they are best kept apart.

This is a fern of rocky places and nearly always from limestone. It is very common on scrubby summits of some hills around Gua Musang in Kelantan.

Asplenium macrophyllum Sw., Schrad. Journ. 1800/2 : 52. 1801; Holtt., Fl. Mal. 2 : 431. 1966.

Found in most parts of Malaya on rocks and as epiphytes. It is common on coastal areas in the east coast and on limestone in Selangor.

Asplenium pellucidum Lam., Encyl. 2 : 305. 1786; Holtt., Fl. Mal. 2 : 428. 1966.

Common in Malaya from the lowlands to the hills, on rocks or as epiphytes; often on limestone.

Asplenium phyllitidis Don, Prodr. Fl. Nep. (1825) 7; Holtt., Fl. Mal. 2 : 420. 1966.

Common in Malaya, usually epiphytic. Recorded from limestone in Kelantan.

Asplenium salignum Bl., Enum. Pl. Jav. (1828) 175; Holtt., Fl. Mal. 2 : 421. 1966.

A. filiceps Copel., Philip. J. Sc. 5c : 285. 1910.

Common in Malaya, usually as an epiphyte, on the lowands, hills and mountains. Fairly common on limestone under partial shade as a low epiphyte or on rocks.

Asplenium squamulatum Bl., Enum. Pl. Jav. (1828) 174; Holtt., Fl. Mal. 2 : 426. 1966.

Distributed throughout Malesia. Recorded in Malaya from Pahang, Kelantan and Selangor, usually on limestone.

Asplenium unilaterale Lam., Encys. 2 : 305. 1786; Holtt., Fl. Mal. 2 : 438. 1966.

Widely distributed in Malaya, on rocks in moist shady places. Uncommon on limestone.

Athyrium cordifolium (Bl.) Copel., Philip. J. Sc. 3c : 300. 1908; Holtt., Fl. Mal. 2 : 548. 1966.

Diplazium cordifolium Bl., Enum. Pl. Jav. (1828) 190.

Common in lowland and mountain forest in Malaya. Recorded only once from limestone.

Athyrium esculentum (Retz.) Copel., Philip. J. Sc. 3c : 295. 1908; Holtt., Fl. Mal. 2 : 562. 1966.

Hemionitis esculenta Retz., Obs. Bot. (1791) 38.

Common in wet places in the lowlands of Malaya. Recorded once from limestone at the base of hill.

Athyrium montanum (v.A.v.R.) Holtt., Fl. Mal. 2 : 555. 1966.

Diplazium montanum v.A.v.R., Bull. Jard. Bot. Ser. II, 28 : 19. 1918.

Common in Malaya in lowland and hill forest. Recorded from limestone in Johore only.

Athyrium pinnatum (Blanco) Copel., Philip. J. Sc. 3c : 297. 1908; Holtt., Fl. Mal. 2 : 560. 1966.

Allantodia pinnata Blanco, Fl. Filip. Ed. 2 (1845) 571.

Widespread in Malaya with one record from limestone.

Athyrium prescottianum (Wall.) Holtt., Fl. Mal. 2 : 557. 1966.

Asplenium prescottianum Wall., Cat. (1829) 235 (nom. nud.)

Endemic, an uncommon species. Recorded once as an epiphyte from limestone.

Blechnum finlaysonianum Hk. et Grev., Ic. Fil. (1831) t. 225; Holtt., Fl. Mal. 2 : 445. 1966.

A common species in lowland and hill forest, once recorded from limestone.

Cyclopeltis crenata (Fée) C. Chr., Ind. Fil. Suppl. 3 : 64. 1934; Holtt., Fl. Mal. 2 : 527. 1966.

Hemicardion crenatum Fée, Gen. Fil. (1852) 283, t. 22A.

Distributed in Burma, S. China and western Malesia. This is a plant of rocky places, usually but not always from limestone, in Malaya. Widely collected from limestone, in part shade.

Davallia denticulata (Burm.) Mett., in Kuhn., Fil. Deck. (1867) 27; Holtt., Fl. Mal. 2 : 359. 1966.

A common rock plant and epiphyte; recorded a number of times from limestone.

Davallia solida (Frost.) Sw., Schrad. Journ. 1800/2 : 87. 1801; Holtt., Fl. Mal. 2 : 360. 1966.

Trichomanes solidum Forst., Prodr. (1786) 86.

A common coastal epiphyte and rock plant in Malaya. Uncommon inland. Recorded only once on limestone; this was from a large local population on the summit of Batu Tapah, growing in part shade on rocks and as a low epiphyte. It is probably not uncommon on limestone, on such dry, rocky, scrubby summits.

Heterogonium alderwereltii Holtt., Sarawak Mus. J. 5 : 163. 1949, Fl. Mal. 2 : 522. 1966.

Pleocnemia membranifolia p.p. quoad Bedd., Handb. Suppl. (1892) 48.

Plant like that of *H. pinnatum*. The typical specimen however has larger sterile fronds with 4–7 pairs of pinnae. The sori is not acrostichoid but is either distinct or elongate along veins. The indusia is distinct though less prominent in mature sori.

Distributed in Sumatra. Restricted to limestone in Malaya (except for a specimen from Patani, Kedah); not as common as *H. pinnatum*.

For notes see under *H. pinnatum*.

Heterogonium pinnatum (Copel.) Holtt., Sarawak. Mus. J. 5 : 163. 1949, Fl. Mal. 2 : 524. 1966.

Stenosemia pinnata Copel., Phil. J. Sc. 1, Suppl. 2 : 48. 1892.

Pleocnemia membranifolia p.p. quoad Bedd. Handb. Suppl. (1892) 48.

Distributed in Sumatra, Borneo and the Philippines. Restricted to limestone in Malaya, and the commonest fern on limestone.

Typically this fern is distinguished from *H. alderwereltii* Holtt. mainly by the absence of indusia and the sterile fronds having only one instead of four to seven pairs of free lateral pinnae. *H. alderwereltii* has distinct sori or extended sori along the veins while typical *H. pinnatum* has acrostichoid sori, and if atypical, the sori extend along veins but still without indusia.

However, there is great variation in the morphology of these two species, thus delimited. There are *H. pinnatum* plants with up to 7 pairs of free pinnae (in the sterile fronds) and which have, in the fertile fronds, an acrostichoid condition in which the sori are non-indusiate. The sterile lamina with up to 7 pairs of free pinnae would seem to belong to *H. alderwereltii* while the acrostichoid non-indusiate sori would seem to belong to *H. pinnatum.* Apart from the extreme forms of *H. pinnatum* in which the sterile fronds have normally one pair of free pinnae, the form and size of the sterile fronds are insufficient characters to separate these two species.

There are identical plants in which the sori are distinct or elongate submarginally. In some instances they are indusiate and in others they are not. Once these two species are kept distinct, one can say that the non-indusiate plants would be abnormal *H. pinnatum* (the normal plants have acrostichoid sori). However, this argument would be equally valid if one says that the non-indusiate condition is found on abnormal *H. alderwereltii* which have lost their indusia. In both indusiate and non-indusiate forms there often exists a condition in which sori are found on fronds with the size and form of a sterile frond. These sori are either very distinct on vein endings or often form submarginal bands.

This range of variation can be found in a single population such as that on the base of Bukit Takun, Selangor, growing on limestone and organic debris. Only the extreme forms would seem to keep these two species apart and I suspect (as Beddome thought) they are variations of one species. This is as much as I can conclude from field observations; experimental culture from spores is required.

Besides these variations there are indusiate as well as non-indusiate forms which are free veined, a character now found in *H. sagenoides* (Mett.) Holtt. Also, the form in which the fertile fronds have a broad lamina and distinct sori encroaches on one of the characters of the remaining species of Heterogonium found in Malaya, *H. saxicolum* (Bl.) Holtt. Other characters, however, seem to keep *H. pinnatum* and *H. alderwereltii* distinct from these latter two species. The former two are also different in being exclusively limestone plants in Malaya with an exception of one specimen of *H. alderwereltii* collected from Patani, Kedah.

In the light of recent collections, the taxonomic status of this complex of *Heterogonium* needs looking into, especially the limestone-inhabiting groups.

For convenience, the two species are retained here, often distinguished only by the presence or absence of an indusium. *H. pinnatum* is the more commonly collected species, appearing on most limestone outcrops except in the extreme north and Kelantan. Both are found in shady, rocky places and most luxuriently in situations with humus accumulation.

It is interesting to note that *H. pinnatum* has been collected from the very small and isolated Johore limestone, forming a link with the more southern Sarawak populations.

Humata heterophylla (Sm.) Desv., Prodr. (1825) 323; Holtt., Fl. Mal. 2 : 366. 1966.
Davillia heterophylla Sm., Mem. Ac. Turin. 5 : 415. 1793.

A widely distributed species in Malaya usually in exposed places, on rocks or as epiphytes. Recorded on limestone from Kelantan.

Humata pectinata (Sm.) Desv., Prodr. (1827) 323; Alston, Phil. J. Sc. 50 : 175 1933; Holtt., Fl. Mal. 2 : 369. 1966.

Davallia pectinata Sm., Mem. Ac. Turin. 5 : 415. 1793.

Distributed from Sumatra to New Guinea, usually on coastal rocks and trees. Inland collections in Malaya are restricted to limestone, growing as low epiphytes or on rocks in shade or part shade. Abundant on the rocky, scrubby summit of Batu Tapah.

Lindsaya lucida Bl., Enum. Pl. Jav. (1828) 216; Holtt., Gard. Bull. S.S. 9 : 131. 1937, Fl. Mal. 2 : 328. 1966.

L. lobbiana Hk. Sp. Fil. 1 : 205. 1848; C. Chr., Gard. Bull. S.S, 4 : 396, 1929; Holtt., Gard. Bull. S.S. 5 : 61. 1930.

In Malaya, a streamside plant of low country, widespread. Recorded once from the base of a limestone hill growing on limestone boulders by a stream.

Microlepia speluncae (L.) Moore, var. *villossima* C. Chr., Gard. Bull. S.S. 4 : 399. 1929; Holtt., Fl. Mal. 2 : 314. 1966.

Nephrolepis biserrata (Sw.) Schott, Gen. Fil. (1834) t. 3; Holtt., Fl. Mal. 2 : 380. 1966.

Aspidium biserratum Sw., Schrad. Jour. 1800/2 : 32. 1801.

A very common fern of open or partly shaded places. Recorded once from limestone (on Gua Musang) as a secondary element about a year and a half after fire destroyed the original vegetation.

Nephrolepis dicksonioides Chr., Verh. Nat. Ges. Basel 11 : 241. 1895; Holtt., Fl. Mal. 2 : 376. 1966.

Distributed in Celebes, Borneo and New Guinea. In Malaya it is restricted to limestone, on exposed or partly exposed situations. Common on many hills and often forming dense thickets.

Nephrolepis falcata (Cav.) C.Chr., Dansk. Bot. Ark. 9 : 15. 1937; Holtt., Fl. Mal. 2 : 381. 1966.

Tectaria falcata Cav., Descr. (1802) 250.

N. barbata Copel., in Holtt., Gard. Bull. S.S. 9 : 132. 1937.

A common fern on rocky places and as epiphytes. Sometimes on limestone.

Nephrolepis hirsutula (Forst.) Pr., Tent. Pterid. (1836) 79; Holtt., Fl. Mal. 2 : 382. 1966.

Polypodium hirsutulum Forst., Prodr. (1786) 81.

Common in Malaya in open places. Recorded once from the disturbed base of limestone in secondary scrub vegetation.

Nephrolepis radicans (Burm.) Kuhn, Ann. Lugd. Bat. 4 : 285. 1869; Holtt., Fl. Mal. 2 : 381. 1966.

Polypodium radicans Burm., Fl. Ind. (1768) 233, t. 66.

Oleandra undulata (Willd.) Ching, Lingnan Sc. Jour. 12: 565. 1933; Holtt., Fl. Mal. 2 : 384. 1966.

Polypodium undulatum Willd., Sp. Pl. 5 : 155. 1810.

A mountain fern, common in Malaya above 1000 m., often on acid peat and humus. An unlikely species to be found on limestone. However, one specimen (Kadim K491) positively of this, is labelled as from Gunong Tempurong, in forest at 250 – 550 m. The main range of mountains which rises abruptly to over 650 m just over a mile to the east of the Gunong Tempurong massive could provide the source for the spread of this species. The plant was probably growing on an accumulation of humus over the limestone.

Polystichum lindsaeifolium Ridl., J. Mal. Br. R. As. Soc. 4 : 61 1926; C. Chr., Gard. Bull. S.S. 4 : 393. 1929; Holtt., Fl. Mal. 2 : 489. 1966.

Endemic to limestone in Selangor, Pahang, Kelantan and Perak, uncommon.

Pteridium aquilinum (L.) Kuhn, *var. wightianum* (Ag.) Tryon, Rhodora 43 : 1-70. 1941; Holtt., Fl. Mal. 2 : 634. 1966.

Pteris aquilina L., Sp. Pl. (1753) 1075.

Pteridium aquilinum (L.) Kuhn, in Holtt., l.c. 389.

Recorded from limestone as a secondary element.

Pteridium caudatum (L.) Maxon var. *yarrabense* Domin, in Tryon, Rhodora 43 : 63. 1941; Holtt., Fl. Mal. 2 : 634. 1966.

Pteris esculenta Forst., Pl. Escul. (1786) 74.

Pteridium esculentum (Forst.) Nakai, Bot. Mag. Tokyo 39 : 109. 1925; Holtt., l.c. 390.

Recorded on limestone as an element of secondary vegetation.

Pteridrys syrmatica (Willd.) C. Chr. et Ching, Bull. Fan Mem. Inst. Bot. 5 : 131. 1934; Holtt., Fl. Mal. 2 : 530. 1966.

Aspidium syrmaticum Willd., Sp. Pl. 5 : 277. 1810.

Distributed in Ceylon, Thailand, Indochina and Malesia to the Philippines. In Malaya, this fern is found mainly in the north and nearly always from limestone. It is a rock fern of shady places.

Pteris ensiformis Burm., Fl. Ind. (1768) 230. Holtt., Fl., 2 : 399. 1966.
Sometimes on limestone.

Pteris longipinnula Wall., Cat. (1829) 108; Holtt., Fl. Mal. 2 : 404. 1966. var. *b*, in Holtt., l.c. 405.

This variety is endemic to Malaya and chiefly from limestone, though not exclusively so. The typical variety is distributed from India to China and southwards throughout Malesia. It differs from the typical variety by the narrower pinnae and by the presence of the branched basal pair of pinnae.

Pteris mertensioides Willd., Sp. Pl. 5 : 394. 1810; Holtt., Fl. 2 : 404. 1966.

Pteris scabripes Wall. apud Hook., Sp. Fil. 2 : 165. 1858; Holtt., Fl. Mal. 2 : 399. 1966.

Endemic, usually on rocks by streams, also in lowland forest and rarely on limestone, not a common species.

Pteris tripartita Sw., Sshrad. Jour. 1800/2 : 67. 1801; Holtt., Fl. Mal. 2 : 408 1966.

P. marginata Bory, Voy. 2 : 192. 1804.

Pteris vittata L., Sp. Pl. (1753) 1074; Holtt., Fl. Mal. 2 : 396. 1966.

Not uncommon on disturbed localities on limestone, by quarry edges and on disturbed summits.

Tectaria amplifolia (v.A.v.R) C. Chr., Ind. Fil. Suppl. 3 : 176. 1934; Holtt., Fl. Mal. 2 : 515. 1966.

Aspidium amplifolium v.A.v.R., Bull. Jard. Bot. Buit. Ser. II, 11 : 2. 1913.

Distributed in Sumatra. Common on and restricted to limestone in Malaya. Apparently unknown from the extreme North-west. A plant of shady places.

Tectaria barberi (Hk.) Copel., Philip. J. Sc. 2c : 414. 1907; Holtt., Fl. Mal. 2 : 508. 1966.

Polypodium barberi Hk., Sp. Fil. 5 : 100. 1864.

Tectaria devexa (Kze) Copel., Philip. J. Sc. 2c : 415. 1907; Holtt., Fl. Mal. 2 : 505. 1966.

Aspidium devexum Kze, Bot. Zeit. (1848) 259.

A. membranaceum Hk., Sp. Fil. 5 : 105. 1864.

Distributed in Ceylon, Thailand and S. China. Restricted to limestone in Malaya, widely distributed and fairly common.

Tectaria griffithii (Bak.) C.Chr., Ind. Fil. (1867) 300; Holtt., Fl. Mal. 2 : 636 1966.

Nephrodium griffithii Bak., Syn. Fil. (1867) 300.

Tectaria multicaudata Ching, Sinensia 2 : 20. 1931; Holtt., F. Mal. 2 : 507. 1966.

T. malayense Christ, Philip. J. Sc. 2c : 187. 1907.

Tectaria macrodonta (Fee) C. Chr., Ind. Fil. Suppl. 3 : 181. 1934; Holtt., Fl. Mal. 2 : 505. 1966.

Sagenia macrodonta Fée, Gen. Fil. (1852) 313 t. 24.

A number of specimens collected from north Malaya are doubtfully identified as this species. One of these is from limestone. They are smaller than the typical form of this species which are represented in India. They resemble *T. variolosa* but the fronds are hairy on both surfaces and hardly dimorphic, and the sori are not all on free veins.

Tectaria variolosa (Wall.) C. Chr., Contr. U.S. Nat. Herb. 26 : 289. 1931; Holtt., Fl. Mal. 2 : 506. 1966.

Aspidium variolosum Wall., Hook., Spec. Fil. 4 : 51. 1862.

Grammitidaceae

Ctenopteris alata (Bl.) Holtt., Fl. Mal. 2 : 232. 1966.

Davallia alata Bl., Enum. Pl. Jav. (1828) 230.

Prosaptia alata Christ, Ann. Buit. II, 5 : 127. 1905.

Ctenopteris moultoni (Copel.) C. Chr. et Tard. Not. Syst. 8 : 181. 1939; Holtt., Fl. Mal. 2 : 229. 1966.

Polypodium moultoni Copel., Philip. J. Sc. 10c : 149. 1915.

Hymenophyllaceae

Trichomanes bipunctatum Poir., in Lamk., Encyl. 8 : 69. 1808; Holtt., Fl. Mal. 2 : 99. 1966.

Crepidomanes bipunctatum Copel., Phil. J. Sc. 67 : 59. 1938.

The only common species of this family (except in the very north) on limestone.

Trichomanes christii Copel., Phil. J. Sc. 1. Suppl. 251. 1906, ibid., 51 : 185. 1933; Holtt., Fl. Mal. 2 : 100. 1966.

Crepidomanes christii Copel., Phil. J. Sc. 67 : 60. 1938.

Trichomanes humile Forst., Prodr., (1786) 84. Copel., Phil. J. Sc. 51 : 164. 1933; Holtt., Fl. Mal. 2 : 98. 1966.

Crepidopteris humilis Copel., Phil. J. Sc. 67 : 58. 1938.

Trichomanes motleyi Bosch, Ned. Kruidk. Arch. 5 : 145. 1861; Copel., Phil. J. Sc. 51 : 201. 1933; Holtt., Fl. Mal. 2 : 92. 1966.

Polypodiaceae

Crypsinus enervis (Cav.) Copel., Gen. Fil. (1947) 207; Holtt., Fl. Mal. 2 : 199. 1966.

Polypodium enervis Cav., Descr. (1802) 245.

Drynaria bonii Christ., Not. Syst. 1 : 186. 1910; Tardieu-Blot et Christ., Fl. Gen. Indochine 7 : 515. 1941.

Rhizome creeping. Nest leaves small, ovate, base cordate-sagittate, margin entire scalloped or shallowly lobed, 5–10 by 3.5–6.5 cm. Foliage leaves with stipes 8–20 cm long, narrowly winged; lamina deeply lobed, 20–45 by 12–20 cm. Lobes 3–7 pairs, 8–20 by 2–4 cm, base decurrent along the rachis. Sori non-indusiate and small, scattered on the lower surface of frond.

Distributed in S. China, Indochina and Thailand. A new record (Chin 1764) for Malaya. Common as low epiphytes and on rocks in Pulau Langgun, Langkawi on the northern side of the island.

Characterised by the small unlobed nest leaves and the dissection of the foliage leaves. The old rhizome which is fleshy and flattened grows up to 3 by 1.5 cm.

Drynaria quercifolia (L.) J. Sm., J. Bot. 3 : 398. 1841; Holtt., Fl. Mal. 2 : 182. 1966.

Polypodium quercifolium Linn., Sp. Pl. (1753) 1087.

Drynaria rigidula (Sw.) Bedd., Ferns Brit. Ind. (1869) t. 314; Holtt., Fl. Mal. 2 : 183. 1966.

Polypodium rigidulum Sw., Schrad. J. 1800/2 : 26. 1801.

A common epiphyte in the northern half of Malaya; it is not found in the south. It is not uncommon on limestone in Langkawi and has been recorded as far south as Bukit Takun in Selangor. This forms the southernmost record for this species in Malaya. On limestone it has been recorded as epiphytes as well as on rocks.

Drynaria sparsisora (Desv.) Moore, Ind. Fil. (1862) 348; Holtt., Fl. Mal. 2 : 183. 1966.

Polypodium sparsisorum Desv., Berl. Mag. 5 : 315. 1811.

Lemmaphyllum accedens (Bl.) Donk. Reinw. 2 : 409. 1954; Holtt., Fl. Mal. 2 : 152. 1966.

Polypodium accedens Bl., Enum. Pl. Jav. (1828) 121.

Weatherbya accedens Copel., Gen. Fil. (1947) 191.

Lepisorus longifolius (Bl.) Holtt., Fl. Mal. 2 : 151. 1966.

Grammitis longifolia Bl., Enum. Pl. Jav. (1828) 119.

Paragramma longifolia Moore, Copel., Gen. Fil. (1947) 190.

Leptochilus decurrens Bl., Enum. Pl. Jav. (1828) 206; Holtt., Fl. Mal. 2 : 164 1966.

Acrostichum variabile Hook, Sp. Fil. 5 : 277. 1864.

Loxogramme avenia (Bl.) Presl., Tent. Pterid. (1836) 215; Holtt., Fl. Mal. 2 : 167. 1966.

Grammitis avenia Bl., Enum. Pl. Jav. (1828) 117.

Loxogramme blumeana Presl., Tent. Pterid. (1836) 215.

Not common on limestone, but recently found to be abundant on the rocky, one-layered scrub forest on the summit of Gua Batu Boh, near Gua Musang, Kelantan; on rocks and as low epiphytes.

Loxogramme scolopendrina (Bory) Presl., Tent. Pterid. (1836) 215; Holtt., Fl. Mal. 2 : 168. 1966.

Grammitis scolopendrina Bory, Dup. Voy. (1829) 257.

Fairly common on limestone and widely distributed.

Microsorium musifolium (Bl.) Ching, Bull. Fan Mem. Inst. 4 : 295. 1933; Holtt., Fl. Mal. 2 : 176. 1966.

Polypodium musifolium Bl., Enum. Pl. Jav. (1828) 134.

Microsorium punctatum (L.) Copel., Univ. Cal. Publ. Bot. 16 : 111. 1929; Holtt., Fl. Mal. 2 : 179. 1966.

Acrostichum punctatum Linn., Sp. Pl. Ed. 2. (1763) 1524.

Photinopteris speciosa (BL.) Presl., Epim. Bot. (1849) 264; Holtt., Fl. Mal. 2 : 187. 1966.

Lomaria speciosa Bl., Enum. Pl. Jav. (1828) 202.

Photinopteris rigida Bedd., Fl. Brit. Ind. (1867) t. 211.

Phymatodes nigrescens (Bl.) J. Sm., Ferns Br. & For. (1866) 94; Holtt., Fl. Mal. 2 : 193. 1966.

Polypodium nigrescens Pl., Enum. Pl. Jav. (1828) 126.

Phymatodes scolopendria (Burm.) Ching, Contr. Inst. Bot. Nat. Acad. Peip. 2 : 63. 1933; Holtt., Fl. Mal. 2 : 191. 1966.

Polypodium scolopendria Burm., Fl. Ind. (1769) 232.

P. phymatodes Linn., Mant. (1771) 306.

Recorded a number of times from limestone, abundant on Batu Tapah, Kelantan, on the scrubby summit growing over boulders and as low epiphytes.

Polypodium papillosum Bl., Enum. Pl. Jav. (1828) 131; Holtt., Fl. Mal. 2 : 203. 1966.

Pyrrosia adnascens (Sw.) Ching, Bull. Chin. Bot. Soc. 1 : 45. 1935; Holtt., Fl. Mal. 2 : 144. 1966.

Polypodium adnascens Sw., Syn. Fil. (1806) 25.

Common in the lowlands of Malaya, epiphytic and on rocks; also common on limestone and widely collected.

Pyrrosia floccigera (Bl.) Ching, Bull. Chin. Bot. Soc. 1 : 71. 1935; Holtt., Fl. Mal. 2 : 147. 1966.

Niphobolus flocciger Bl., Enum. Pl. Jav. (1828) 107.

Fairly common in Malaya, usually from 300–1300 m, in partly shaded areas, epiphytic. Recorded once from limestone at less than 100 m elevation (UNESCO 1962, 216, from Gua Batu Boh, Kelantan).

Pyrrosia penangiana (Hook.) Holtt., Fl. Mal. 2 : 146. 1966.

Niphobolus penangianus Hook., Ic. Pl. (1840) t. 203.

Distributed in Sumatra. Recorded from the northern half of Malaya, usually on limestone; on rocks or as epiphytes.

Pyrrosia stigmosa (Sw.) Ching, Bull. Chin. Bot. Soc. 1 : 67. 1935; Holtt., Fl. Mal. 2 : 148. 1966.

Polypodium stigmosum Sw., Schrad. Jour. 1800/2 : 21. 1801.

Distributed in North India and Indochina and from Sumatra to New Guinea. Restricted to limestone in Malaya, on rocks and epiphytic; it has been reported as an epiphyte on Rain trees near Gua Batu, Selangor.

Pyrrosia varia (Kaulf.) Farwell, Am. Midl. Nat. 12 : 302. 1931; Holtt., Fl. Mal. 2 : 146. 1966.

Niphobolus varius Kaulf., Enum. Fil. (1824) 125.

A widely distributed species, also common on limestone.

Schizaeaceae

Lygodium flexuosum (L.) Sw., Schrad. Jour. 1800/2 : 106. 1801; Holtt., Fl. Mal. 2 : 57. 1966.

Ophioglossum flexuosum Linn., Sp. Pl. (1753) 1063.

Lygodium polystachyum Wall. ex Moore, Gard. Chron. (1859) 671; Holtt., Fl. Mal. 2 : 56. 1966.

Distributed in Burma and Thailand. Uncommon and apart from specimens from Penang Hill (granite), this species is restricted to limestone in Malaya. Recorded from Perak, Kelantan, Langkawi and Pahang, usually in shady forest.

Schizaea inopinata Selling, Sevensk Bot. Tidskr. 40 : 274. 1946; Holtt., Fl. Mal. 2 : 52. 1966.

Distributed in Sumatra and Philippines. In Malaya, this species is restricted to limestone in Kelantan, Pahang and Selangor, not uncommon. It resembles the common *S. digitata* (L.) Sw. and is frequently mistaken for it. *S. inopinata* is however characterized by having the sporangia in two instead of four rows.

Thelypteridaceae

Abacopteris urophylla (Wall.) Ching, Bull. Fan Mem. Inst. Bot. 8 : 251. 1938; Holtt., Fl. Mal. 2 : 296 1966.

Polypodium urophyllum Wall., in Hook., Sp. Fil. 5 : 9. 1863.

Cyclosorus extensus (Bl.) Ching, Bull. Fan Mem. Inst. Bot. 8 : 182. 7938; Holtt., Fl. Mal. 2 : 264. 1966.

Aspidium extensum Bl., Enum. Pl. Jav. (1828) 156.

Cyclosorus interruptus (Willd.) Ching, Bull. Fan Mem. Inst. Bot. 8 : 184. 1938; Holtt., Fl. Mal. 2 : 262. 1966.

Pteris interrupta Willd., Phytogr. 1 : 13. 1794.

Cyclosorus megaphyllus (Mett.) Ching, Bull. Fan Mem. Inst. Bot. 8 : 225. 1938; Holtt., Fl. Mal. 2 : 268. 1966.

Aspidium megaphyllum Mett., Ann. Mus. Lugd. Bat. 1 : 233. 1864.

Cyclosorus unitus (L.) Ching, Bull. Fan Mem. Inst. Bot. 8 : 192. 1938; Holtt., Fl. Mal. 2 : 260. 1966.

Polypodium unitum L., Syst. Nat. ed. 10, 2 : 1326. 1759.

Thelypteris immersa (Bl.) Ching, Bull. Fan Mem. Inst. Bot. 6 : 306. 1936; Holtt., Fl. 2 : 243. 1966.

Aspidium immersum Bl., Enum. (1828) 156.

GYMNOSPERMS

Araucariaceae

Agathis dammara (Lambert) L. G. Rich., Comm. Bot. Conif. Cycad. (1826) 83; Keng, Tree Fl. Mal. 1 : 41. 1972.

A. loranthifolia Salisb. in Ridl., Flora 5 : 278. 1925.

A. alba (Lam.) Jeff. in Burk., Dict. I : 62. 1935. Corner, Ways. Trees I : 715. 1940.

Usually found on the hills; once recorded (Loh FRI 17201) for limestone at 600–700 m at Gua Peringat, Pahang. This was growing in deep soil in a gully.

Cycadaceae

Leaves with petioles about 100 cm long, leaflets 0.7–0.9 cm wide. Male cone about 20 cm long .... *Cycas siamensis*
Leaves with petioles about 200 cm long, leaflets 1.3–2.0 cm wide. Male cone about 35 cm long .... *Cycas rumphii*

Cycas rumphii Miq., Bull. Sc. Phys. Neerl. 839, 45; Hk. f., F.B.I. 5 : 657; Ridl., Fl. 5 : 284. 1925.

Cycas siamensis Miq., Bot Zeit. (1863) 334; Hk. f., F.B.I. 5 : 657; Ridl. Fl. 5 : 285. 1925.

Distributed in Burma and Thailand; in Malaya, restricted to limestone, and common on Langkawi islands.

Gnetaceae

A shrub or small tree, to 3 m tall; flowers not embedded in thick hair masses. .... *Gnetum gnemon* var. *tenerum*
A liana, more than 10 m long; flowers embedded in thick hair masses. .... *Gnetum cuspidatum*

Gnetum cuspidatum Bl., Rumphia 4 : 5. 1848; Henders., J. Mal. Br. As. Soc. 17 : 87. 1939; Markgraf, Fl. Mal. I, 4 : 343. 1951.

G. penangense Ridl., Fl. 5 : 276. 1925.

Gnetum gnemon Linn., Mant. 1 : 125. 1767; Markgraf, Bull. Jard. Bot. Btzg III, (10) : 436. 1930; Ridl. Fl. 5:273. 1925; Markgraf, Fl. Mal. I, 4 : 340. 1951.

var. *tenerum* Markgraf, Fl. Mal. I, 4 : 341. 1951.

Podocarpaceae

Male cones 3–5 together. Leaves 2.5–10 by 0.5–1 cm .... *Podocarpus polystachyus*
Male cones solitary or sometimes 2–3 together. Leaves usually larger, 5.5–20 by 0.7–1.5 cm .... *Podocarpus neriifolius*

Podocarpus polystachyus R. Br. [in Mirb., Mem. Mus. Hist. nat. Paris 13:47. 1825 nom. nud.] ex Endl., syn. Conif. (1847) 215. Ridl., Fl. 5 : 282. 1925; Keng, Tree Fl. Mal. 1 : 53: 1972.

Usually coastal except on limestone hills where it is very widely distributed and common.

Podocarpus neriifolius D. Don, in Lambert, Desc. Gen. Pinus 1 : 21. 1824; Ridl., Fl. 5 : 281. 1825; Keng, Tree Fl. Mal. 1 : 51. 1972.

Usually on hill and mountain forest, rarely below 300 m. Recorded on limestone from Gua Batu Selangor. (Ng FRI. 1634).

A List of Holttum's New Taxa and Name-Changes in Ferns to July 1975

by

J. A. Crabbe

British Museum (Natural History)

London

Little did I think, when I embarked on this abstracting, that I would be delving among some 420 titles by R. E. Holttum which range over botany, horticulture, philosophy, etc. (see Flora Malesiana Bulletin 28: 1975), and that I would find around 700 items for this present list.

I have not included anything published after his 80th birthday on 20 July 1975, nor some few names superfluously replicated, nor some invalidly published (usually without latin diagnoses and usually rectified later). The genus *Polystichopsis* (17: 149, 152) is, to me, obscure and I suspect there may be other items in this work and also in a similar treatment (The classification of ferns, in Biol. Rev. 24: 267–296. 1949).

It is with the greatest pleasure that I present this list, acknowledging with gratitude much helpful discussion with colleagues, and trusting it will serve a useful purpose.

For brevity, I have numbered the bibliography, then quoted those numbers followed by page numbers. New species give the type and its location, a semicolon separating holotype from isotypes. Where Holttum designates no type but lists specimens he has seen, I have quoted the first in that list, not thereby implying any other status. Basionym authors followed by their genus are enclosed in round brackets.

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A. salicifolia (Wall. ex Hook. — Meniscium) 24:288

Alsophila parvifolia 2:19. — Mentawi Is., Kloss 14579 (SING)

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A. bergiana var. tristanensis 57:134. — Tristan da Cunha, Carmichael (K)
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A. riparium (Holtt. — Diplazium) 24:554
A. simplicivenium (Holtt. — Diplazium) 24:573
A. subintegrum (Holtt. — Diplazium) 24:557
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B. singaporensis 16:271. — Malaya, Hullett s.n., March 1882, 2 sheets (SING)

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C. perrigida (v.A.v.R. — Phegopteris) 60:27
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C. pseudoferox 60:24. — Malay Peninsula, Perak, Matthew s.n., 6 Feb 1908 (K)
C. sambasensis 60:24. — W Borneo, Brooks s.n. Sept 1908 (BM; K, L)
C. urens 60:28. — Philippine Is., Luzon, Mt Makiling, Price 2367 (PNH; K)

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Bibliography

(dates of publication given here may differ from those given on title-pages)

1 A new fern from the Malay Peninsula. *Gdns' Bull. S.S.* **4**: 56–57. (1927).
2 Spolia Mentawiensia: Pteridophyta. *J. Mal. Br. R. Asiatic Soc.* **6**: 14–23. (1928).
3 New species of ferns from the Malay Peninsula. *Gdns' Bull. S.S.* **4**: 408–410. (1929).
4 The genus Lindsaya in the Malay Peninsula, with descriptions of two new species. *Gdns' Bull. S.S.* **5**: 58–71. (1930).
5 Aspidium maingayi (Baker) Holttum comb. nov. *Gdns' Bull. S.S.* **5**: 207–211. (1931).
6 On Stenochlaena, Lomariopsis and Teratophyllum in the Malayan Region. *Gdns' Bull. S.S.* **5**: 245–313. (1932).
7 The ferns of Mt. Kinabalu (C. Christensen & R.E.H.). *Gdns' Bull. S.S.* **7**: 191–324. (1934).
8 The tree-ferns of the Malay Peninsula. *Gdns' Bull. S.S.* **8**: 293–320. (1935).
9 Notes on Malayan ferns, with descriptions of 5 new species. *Gdns' Bull. S.S.* **9**: 119–138. (1937).
10 Further notes on Stenochlaena, Lomariopsis and Teratophyllum. *Gdns' Bull. S.S.* **9**: 139–144. (1937).
11 The genus Lomagramma. *Gdns' Bull. S.S.* **9**: 190–221. (1937).
12 A re-definition of the genus Teratophyllum. *Gdns' Bull. S.S.* **9**: 355–362. (1938).
13 The genus Lomariopsis in Madagascar and the Mascarene Islands. *Notulae Systematicae,* Paris **8**: 48–62. (1939).
14 New species of Lomariopsis. *Kew Bull.* **1939**: 613–628. (1940).
15 The fern genus Diplazium in the Malay Peninsula. *Gdns' Bull. S.S.* **11**: 74–108. (1940).
16 New species of vascular plants from the Malay Peninsula. *Gdns' Bull. Sing.* **11**: 267–298. (1947).
17 A revised classification of Leptosporangiate ferns. *J. Linn Soc. Bot.* **53**: 123–158. (1947).
18 The fern-genus Heterogonium Presl. *Sarawak Museum J.* **5**: 156–166. (1949).
19 Further notes on the fern-genus Heterogonium Presl. *Reinwardtia* **1**: 27–31. (1950).
20 The fern-genus Pleocnemia Presl. *Reinwardtia* **1**: 171–189. (1951).
21 The fern-genus Arcypteris Underwood (Dictyopteris Presl sensu Fée). *Reinwardtia* **1**: 191–196. (1951).
22 A new Malayan Athyrium. *Kew Bull.* **8**: 545. (1954).

23 A new fern from Malaya (Athyrium angustipinna). *Gdns' Bull. Sing.* **14**: 8. (1953).

24 *A revised Flora of Malaya* vol. 2. *Ferns of Malaya.* Singapore: Government Printing Office. (1955).

25 Some additional species of Heterogonium. *Reinwardtia* **3**: 269–274. (1955).

26 Florae Malesianae Praecursores, XVI: On the taxonomic subdivision of the Gleicheniaceae, with descriptions of new Malaysian species and varieties. *Reinwardtia* **4**: 257–280. (1957).

27 Notes on Malaysian ferns, with descriptions of a new genus and new species. *Kew Bull.* **13**: 447–455. (1959).

28 *Flora Malesiana,* Ser. II, Pteridophyta, vol. 1, pt. 1: i–xxiii, 1–61. (Introductory Note; List of genera of Malayan Pteridophyta; The Morphology of Ferns; General Keys 1 & 2; Keys to Genera; Bibliography; Gleicheniaceae, Schizaeaseae). (1959).

29 Two problem-species: Schizoloma cordatum Gaud. and Syngramma pinnata J. Sm. *Amer. Fern J.* **50**: 109–113. (1960).

30 New species of tree-ferns (Cyathea Sm. and Dicksonia L'Herit). *Kew Bull.* **16**: 51–64. (1962).

31 New species of Malaysian ferns. *Blumea* **11**: 529–534. (1963).

32 Cyatheaceae. *Flora Malesiana,* Ser. II, **1**, pt. 2: 65–176. (1963).

33 The tree-ferns of the genus Cyathea in Australasia and the Pacific. *Blumea* **12**: 241–274. (1964).

34 Cytological observations on ferns from New Guinea, with descriptions of new species (R.E.H. & S. K. Roy). *Blumea* **13**: 129–139. (1965).

35 Tree-ferns of the genus Cyathea Sm. in Asia (excluding Malaysia). *Kew Bull.* **19**: 463–487. (1965).

36 Studies in the Flora of Thailand 33: Filicinae excl. of the Ophioglossaceae (second list). *Dansk Bot. Ark.* **23**: 227–244. (1965).

37 The genera Lomariopsis, Teratophyllum and Lomagramma in the islands of the Pacific and Australia. *Blumea* **14**: 215–223. (1966).

38 Two new species of Lomagramma from New Guinea. *Blumea* **14**: 224. (1966).

39 The genus Arthropteris J. Sm. in Malesia. *Blumea* **14**: 225–229. (1966).

40 Florae Malesianae Precursores XLIV: The fern-genus Elaphoglossum in Malesia, with descriptions of new species. *Blumea* **14**: 317–326. (1967).

41 Four new species of ferns from New Guinea. *Blumea* **14**: 327–329. (1967).

42 New ferns from Malesia. *Kew Bull.* **20**: 455–460. (1967).

43 Studies in the Flora of Thailand 38: Some plants new or rare to Thailand with descriptions of new species: Filicinae. *Dansk Bot. Ark.* **23**: 308–309. (1966).

44 Botanical Report of the Danish Noona Dan Expedition, Filicinae. *Dansk Bot. Ark.* **25**: 35–52. (1967).

45 *A revised Flora of Malaya* vol. 2. *Ferns of Malaya,* ed. 2. Singapore: Government Printing Office. (1968).

46 A re-definition of the fern-genus Taenitis Willd. *Blumea* **16**: 87–95. (1968).

47 A commentary on some type specimens of ferns in the Herbarium of K. B. Presl. *Novitates Botanicae Inst. Bot. Univ. Carol. Prag.* 1968: 3–57. (1969).

48 Studies in the family Thelypteridaceae 1. The genera Phegopteris, Pseudophegopteris and Macrothelypteris. *Blumea* **17**: 5–32. (1969).

49 New species of Thelypteridaceae from India, Ceylon and Burma (R.E.H. & P. Chandra). *Kew Bull.* **26**: 79–82. (1971).

50 Studies in the family Thelypteridaceae 3. A new system of genera in the Old World. *Blumea* **19**: 17–52. (1971).

51 The genus Stenochlaena J. Sm., with description of a new species. *American Fern J.* **61**: 119–123. (1971).

52 Morphology and anatomy of the genera Davallia, Araiostegia and Davallodes, with a discussion on their affinities. (T. & U. Sen & R.E.H.). *Kew Bull.* **27**: 217–243. (1972).

53 Studies in the family Thelypteridaceae 4. The genus Pronephrium Presl. *Blumea* **20**: 105–126 (1972).

54 The identity of three type specimens in the Willdenow Herbarium. *Amer. Fern J.* **63**: 81–84 (1973).

55 Studies in the family Thelypteridaceae 5. The genus Pneumatopteris Nakai. *Blumea* **21**: 293–325. (1974).

56 Studies in the family Thelypteridaceae 6. [The genera] Haplodictyum and Nannothelypteris. *Kalikasan* **2**: 58–68. (1974).

57 Thelypteridaceae of Africa and adjacent islands. *S. African J. Bot.* **40**: 123–168. (1974).

58 Additions to the Fern Flora of Java. *Reinwardtia* **8**: 499–501. (1974).

59 The genus Trigonospora (Thelypteridaceae) in Malaysia. *Reinwardtia* **8**: 503–507. (1974).

60 Studies in the family Thelypteridaceae 7. The genus Chingia. *Kalikasan* **3** : 13–28. (1974).

61 The fern-genus Pleocnemia. *Kew Bull.* **29**: 341–357. (1974).

62 [new thelypterid nomenclatural combinations] in B. K. Nayar, *A revised nomenclature of the thelypteridoid ferns.* pp 202–212 in B. K. Nayar & S. Kaur, Companion to R. H. Beddome's Handbook to the ferns of British India, Ceylon and the Malay Peninsula. Koenigstein & New Delhi (1974).

63 Studies in the family Thelypteridaceae 8. The genera Mesophlebion and Plesioneuron. *Blumea* **22**: 223-250 (1975).

64 New Philippine ferns. *Kalikasan* **3**: 196–197 (1975).

65 Studies in the family Thelypteridaceae 9. The genus Sphaerostephanos in the Philippines. *Kalikasan* **4**: 47–68 (1975).

Philippine Dryopteris

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Summary

A key to the thirteen recognized Philippine species of *Dryopteris* is presented, with descriptions of two new species, *D. uropinna* and *D. permagna,* and four species not hitherto reported as Philippine: *D. chrysocoma, D. pulvinulifera, D. polita,* and *D. formosana. Ctenitis mearnsii* is reduced to *Nothoperanema hendersonii.*

The genus *Dryopteris* Adanson (nom. cons.) is here circumscribed in the strict sense adopted by most recent authors, with its nearest relatives in Asia being along one lineage *Arachniodes* and on another *Nothoperanema. Dryopteris* consists of about two hundred species, mostly north subtropical and temperate, with the centre of diversity the Himalayan-East Asian region. Distinguishing characters of the genus are:

Rhizome short-erect, infrequently short-creeping, stipes with 5 or more vascular bundles at base, axes grooved above, junctions between grooves of different orders of axes open, lamina pinnate to quadripinnate, architecture usually anadromous at proximal base, then catadromous upwards and outwards, or infrequently anadromous throughout. Hairs not acicular, nor multicellular and erect, margins not bearing long sharp cartilaginous teeth, sinuses without cartilaginous membranes or protuberances, veins free, not reaching margin. Sori along veins, round, receptacles strongly raised, indusium round-reniform with a short sinus, somewhat stalked (rarely much reduced), paraphyses usually present, spores monolete, variously winged, bullate, or tuberculate.

Arachniodes is always rather strongly anadromous throughout, with dimidiate pinnules (basiscopic base excised), and usually with sharp cartilaginous teeth. It is, however, extremely difficult to formulate a verbal boundary; among Philippine plants *Arachniodes hasseltii* has blunt or rounded segments and *Dryopteris pulvinulifera* and *D. subarborea* are anadromous.

Nothoperanema has often been immersed in *Dryopteris* or *Ctenitis*. It agrees with *Dryopteris* in soral characters but is vegetatively similar to *Peranema* and *Diacalpe*, and thence to *Acrophorus* and *Stenolepia*. The patent stipe paleae, erect *Diacalpe*, and thence to *Acrophorous* and *Stenolepia*. The patent stipe paleae, erect conical multiseptate hairs on lamina, and fine dissection clearly mark the genus. It might more properly be reduced to *Peranema* (as has *Diacalpe*) than *Dryopteris*. Since *Nothoperanema* has not been reported by name from the Philippines, I provide below a brief synonymy and description of the one Philippine species:

Nothoperanema hendersonii (Bedd.) Ching, Acta Phytotax. Sinica 11 (1966) 28. —— *Lastrea hendersonii* Bedd., Ferns Brit. India Suppl. (1876) 17, t. 377. —— *Dryopteris hendersonii* (Bedd.) C. Chr., Ind. Fil. (1905) 270; Tagawa, Acta Phytotax. Geobot. 6 (1937) 155. —— *Ctenitis mearnsii* Copel., Philip. J. Sci. 81 (1952) 24; Fern Fl. Philip. 2 (1960) 289.

Rhizome ascending, paleae brown, to 18 × 3 mm, concolorous, with minute marginal projections. Stipes bright brown, to 70 cm long and 8 mm thick at base, paleae linear, patent, brown, subentire. Lamina subquadripinnate, to 70 cm long, ovate-deltoid, anadromous in sequence of pinnules at base, upwards catadromous, rachis with reduced linear patent paleae, these grading to stout conical erect multiseptate hairs forming a tuft inside rachis groove at junctions, also along costae, costules, and veins both sides of lamina; texture thin papyraceous. Basal pinnae to 30 cm long, stalk 3 cm, apex acuminate; basal basiscopic pinnule to 9 cm, secondary pinnules very deeply lobed. Middle pinnae ascending, 12-17 cm long, acuminate, stalk 5-10 mm, basal pinnules c. 3 × 1.7 cm, secondary pinnules adnate, blunt, shallowly lobed or crenate-serrate, apex toothed. Sori inframedial, indusium dark brown, minutely farinose, 0.7 mm across.

LUZON. Mt Pulog, *Curran et al. FB 16277* (MICH), *Jacobs 7301* (A, CAHUP, PNH); Mt Burnay, *Iwatsuki et al. P-774;* Benguet, Pauai, *McGregor BS 8507* (MICH); Haight's Place, *Mearns BS 4216* (MICH), *4218* (MICH); Mt Singakalsa, *Celestino & Castro PNH 3971* (MICH); Mt Santo Tomas, *Price 1868;* Bulasan, *Copeland s.n.* 7 May 1913 (MICH).

Ecology: Terrestrial in mountain forests, 1900-2700 m.

Distribution: N. India, Nepal, S. China, Japan, Thailand, Java.

Most of the Philippine species of *Dryopteris* are found in the Benguet highlands of Luzon; none were collected by botanists until the 1890s. It is likely that additional species remain to be discovered in the mountains of northern Luzon.

Aside from the delimitation of *Dryopteris* from *Arachniodes*, the greatest difficulty still remaining is the proper treatment of the *D. subarborea* complex (species 11-13 below). There are at least three Philippine taxa but their relationship with plants from elsewhere in Malesia and Polynesia remains to be ascertained. I am not sure that I have applied the names *D. subarborea* and *D. purpurascens* correctly.

Instead of a full synonymy, I have provided all Philippine references, original and basionym citations, and reference to important descriptions. Philippine specimens I have seen are cited; duplicates of my own collections are being distributed. Ecological information is based on Philippine conditions.

KEY TO THE PHILIPPINE SPECIES OF *DRYOPTERIS*

1. Indusium c. 2 mm across, persistently helmet-shaped; rhizome paleae orange-colored
    2. Fronds dimorphic (the fertile lamina contracted), deltoid-ovate, not glandular .... **1**. *D. cochleata*
    2. Fronds uniform, lanceolate, bearing small capitate glandular hairs on axes, lamina, and indusia .... **2**. *D. chrysocoma*
1. Indusium exceptionally to 1.5 mm across, shriveling; paleae not orange
    3. Lamina lanceolate or narrower, pinnate or bipinnatifid; basal pinnae similar to middle pinnae
        4. Pinnae toothed or shallowly lobed .... **3**. *D. hirtipes*
        4. Pinnae lobed nearly to costa .... **4**. *D. wallichiana*
    3. Lamina ovate or deltoid-ovate, at least bipinnate; basal pinnae more dissected than middle pinnae, considerably longer and/or broader

5. Lamina to c. 50 cm long
    6. Lamina anadromous throughout; rhizome short-creeping, paleae golden-brown, acicular .... **5**. *D. pulvinulifera*
    6. Lamina catadromous above base; rhizome short-erect, paleae brown or black
        7. Stalks of basal pinnae over 15 mm long; indusium minute .... **6**. *D. polita*
        7. Stalks of basal pinnae 10 mm or less long; indusium evident
            8. Paleae of rhizome and stipe pale brown, very thin, lanceolate or ovate; rachis groove strongly papillate within .... **7**. *D. sparsa*
            8. Paleae at least partially black, not thin, linear or narrowly lanceolate; rachis groove not papillate
                9. Basal basiscopic pinnule of basal pinnae about equal to succeeding basiscopic pinnules .... **8**. *D. uropinna*
                9. Basal basiscopic pinnule much enlarged
                    10. Pinnules mostly somewhat falcate (costules ascendingly curved) .... **9**. *D. varia*
                    10. Pinnules never falcate (costules not arcuate) .... **10**. *D. formosana*
5. Lamina over 100 cm long
    11. Rhizome short-creeping; lamina glabrous .... **11**. *D. subarborea*
    11. Rhizome short-erect; lamina with appressed multi-cellular hairs beneath
        12. Sori containing conspicuous paraphyses with large yellow cylindric heads .... **12**. *D. purpurascens*
        12. Paraphyses inconspicuous, hyaline, shorter than sporangia, heads not or only very slightly expanded .... **13**. *D. permagna*

1. **Dryopteris cochleata** (Don) C. Chr., Ind. Fil. (1905) 258; Ching, Bull. Fan Mem. Inst. Biol. Bot. 8 (1938) 434; Copel., Fern Fl. Philip. 2 (1960) 282. —— *Nephrodium cochleatum* Don, Prod. Fl. Nepal. (1825) 6. —— *D. heleopteroides* Christ, Philip. J. Sci. 2C (1907) 212; Merrill & Merritt, Philip. J. Sci. 5C (1910) 317.

LUZON. Benguet, *Bacani FB 15962* (MICH), *Copeland 1837a* (MICH), *Hernaez CAHUP 13898, Price 1146, 1823, 1827, Ramos BS 5813* (NY, US, MICH), *Williams 1502* (NY, US); Bontoc, *Vanoverbergh 3343* (F); Ilocos Norte, *Iwatsuki et al. P-113, P-151, P-221, Price 3341.*

Ecology: Rhizome short-creeping, terrestrial or on limestone, 200-1800 m, in fairly open seasonally dry grassland, under pine forest, or at borders of secondary growth, in sites with good drainage, cool nights, and no wind.

Notes: Copeland described *D. cochleata* as glabrous but the lamina beneath has appressed multicellular hairs identical to apices of paleae.

Distribution: S. China (not Taiwan), India, Nepal, Burma, Thailand, N. Vietnam, Java, Bali.

2. **Dryopteris chrysocoma** (Christ) C. Chr. Ind. Fil. (1905) 257; Ching, Bull. Fan Mem. Inst. Biol. Bot. 8 (1938) 436. —— *Aspidium filix-mas* var. *chrysocoma* Christ, Bull. Herb. Boiss. 6 (1898) 966.

Rhizome short-creeping, paleae c. 1.5 cm long, narrow, orange-brown, concolorous, cells very long and slender, margins with minute regular projections. Stipe 20 cm × 3 mm, stramineous, bearing broadly ovate paleae 5 × 2.5 mm and reduced narrow paleae. Lamina lanceolate, 35 × 15 cm, bipinnate throughout, thick herbaceous, catadromous except at base, both surfaces and axes bearing erect capitate orange glandular hairs, rachis beneath also with narrow orange-brown paleae. Pinnae linear-lanceolate, basal slightly reduced, 17 pairs, to 9 × 2.7 cm, abruptly narrowed to the acute apex. Pinnules c. 12 × 6 mm, sessile but not adnate (base narrow), apices broad, rounded, with numerous small teeth. Indusia 2.5 mm across, persistent, convex, orange-brown, bearing numerous capitate orange glandular hairs.

LUZON. Benguet, Haight's Place, July 1907, *Mearns BS 4219* (MICH).

Ecology: Terrestrial, c. 2100 m; only one Philippine collection.

Notes: Very small plants may be fertile.

Distribution: S. China, N. India & Pakistan, Burma. Reported from Taiwan by Tagawa, Acta Phytotax. Geobot. 8 (1939) 22, but not mentioned in the recent Flora of Taiwan.

3. **Dryopteris hirtipes** (Bl.) O. Ktze., Rev. Gen. Pl. 2 (1891) 813; Christ, Philip. J. Sci. 2C (1907) 212; Merrill & Merritt, Philip. J. Sci. 5C (1910) 317; Copel., Leafl. Philip. Bot. 3 (1910) 806; Fern Fl. Philip. 2 (1960) 281; Holttum, Ferns of Malaya, ed. 2 (1966) 635; Sledge, Bull. Brit. Mus. (Nat. Hist.) Bot. 5 (1973) 6. —— *Aspidium hirtipes* Bl., Enum. Pl. Jav. (1828) 148; Christ, Bull. Herb. Boiss. 6 (1898) 194. —— *Nephrodium hirtipes* (Bl.) Hook.; Copel., Polyp. Philip. (1905) 21.

LUZON. Bontoc, *Vanoverbergh 3146* (F); Mt Data, *Copeland 1887* (MICH), *Price 389, 395, 402;* Mt Pulog, *Celestino et al. PNH 3026* (MICH), *Curran et al. FB 16278* (MICH); Mt Polis, *Price 422, 436;* Mt Singakalsa, *Celestino & Castro PNH 3981* (MICH); Mt Santo Tomas, *Price 1006, Topping 1187* (NY); Pauai, *J. K. Santos BS 31667* (US); Benguet, *Elmer 6529* (NY, US), *Price 1672, Topping 248* (GH, US), *302* (GH, US), *303* (MICH, US), *311* (NY, US); Mt Ragut, *Loher 850* (US).

MINDANAO. Davao, Mt Calelan, *Elmer 10799* (F, GH, MICH, NY, US); Mt Apo, *Copeland s.n.* 27 Oct 1904 (MICH); Cotobato, Mt Matutum, *Copeland s.n.* 1 May 1917 (MICH).

Ecology: Terrestrial in mountain forest, 1350-2650 m.

Notes: Dimensions more variable than hitherto reported, in Philippine material stipes 12–63 cm, lamina 14–73 cm long, pinnae 2.3–24 × 0.8–3.5 cm. *Topping 311* at NY is aberrant in having irregularly anastomosing veins. Reports of this species from Mt Arayat (Christ 1898, Copeland 1905, 1960) are based on erroneous localization of *Loher 850*, Feb. 1894, by Christ (1898); the specimen in US bears the same date and elevation (1950 m) as Christ's published report but with the name Mt Ragut. Arayat is only about 1000 m high.

Distribution: Sri Lanka and India to S. China & Japan, Malesia, Samoa.

4. **Dryopteris wallichiana** (Spreng.) Hyl., Bot. Notis. 1953 (1953) 352; Alston, Amer. Fern J. 47 (1957) 92; Sledge, Bull. Brit. Mus. (Nat. Hist.) Bot. 5 (1973) 8. —— *Aspidium wallichianum* Spreng., Syst. Veget. 4 (1827) 104. —— *D. filix-mas* var. *parallelogramma* (Kunze) Christ, Philip. J. Sci. 2C (1907) 212; Merrill & Merritt, Philip. J. Sci. 5C (1910) 317. —— *D. paleacea* (Sw.) C. Chr. nom. illegit.; Copel., Fern Fl. Philip. 2 (1960) 281.

LUZON. Mt Pulog, *Curran et al. FB 16247* (MICH), *Jacobs 7260* (A, CAHUP, PNH); Mt Data, *Copeland 1875* (MICH).

Ecology: Terrestrial in wet mountain forest, 2100–2800 m.

Notes: Alston (1957) distinguished the tropical American *D. parallelogramma* from the Asian *D. wallichiana* by only the color of the rhizome scales, which I find to be unreliable. Christensen, Cont. U. S. Nat. Herb. 26 (1931) 280, stated: "... a close comparison of very complete specimens ... has shown me that it is impossible to find one stable character by which they may be distinguished." The genus *Dichasium* (A. Br.) Fée was established for plants of this species.

Distribution: Sri Lanka, India, Nepal, Burma, S. China & Taiwan, Japan, Java, N. Borneo, New Guinea, Hawaii, Mexico, Cuba, Jamaica, Hispaniola, Guatemala, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia, Argentina, Rhodesia, Madagascar.

5. **Dryopteris pulvinulifera** (Bedd.) O. Ktze. Rev. Gen. Pl. 2 (1891) 813; Ching, Bull. Fan Mem. Inst. Biol. Bot. 8 (1938) 466; Sledge, Bull. Brit. Mus. (Nat. Hist.) Bot. 5 (1973) 10. —— *Lastrea pulvinulifera* Bedd., Ferns Brit. Ind. (1870) t. 333.

Rhizome short-creeping, paleae very narrow, bright golden-brown, glossy, c. 1 cm long, entire. Stipe bases swollen, fleshy, blackish, densely paleate; stipes to 34 cm long. Lamina deltoid-ovate, acuminate, to 49 cm long, tripinnate + pinnatifid at base, anadromous throughout, both surfaces with multiseptate dark appressed hairs and unicellular glossy hyaline appressed glandular hairs, rachis and costae with lanceolate blackish subclathrate paleae grading distally to bullate based. Pinnae to 18 free pairs, basal pinnae to 22 cm long, basal basiscopic pinnule to 7 cm long; larger pinnae gradually acuminate, pinnules acute, teeth of segments acute (not aristate nor cartilaginous). Sori subterminal on veins, about medial, indusia c. 1 mm across, reddish-brown, with multicellular hairs at base of sinus and minute fragile appressed glossy glandular hairs elsewhere and at margins.

LUZON. Mt Data, *Copeland 1861* (MICH); Mt Santo Tomas, *Price 1616, 1841*; Mt Burnay, *Iwatsuki et al. P-827, P-848, Price 3363.*

Ecology: Terrestrial, rarely petrophytic among mosses, 1800–2200 m, on slopes and cliffs in mossy forest.

Notes: Extremely small fronds may be fully fertile; the smallest, such I have seen, is 4.5 cm long including stipe.

Distribution: Sri Lanka, N. E. India, Nepal.

6. **Dryopteris polita** Rosest., Fedde Repert. 13 (1914) 218; Holttum, Ferns of Malaya (1955) 492; DeVol & Kuo, Fl. Taiwan 1 (1975) 378.

Rhizome short-erect, paleae glossy, light brown, subentire, concolorous, to 13 × 2 mm. Stipe to 52 cm by 3 mm, stramineous. Lamina lanceolate-deltoid, 18–45 cm long, catadromous above base, bipinnate, texture firm herbaceous, beneath with multiseptate appressed reddish-brown hairs, axes with sparse narrow fibrils. Pinnae narrowly lanceolate, acuminate, evenly tapering, broadest on basiscopic side; basal pinnae to 17 cm long, stalks 1.6–3.6 cm long, largest basal basiscopic pinnule to 6.8 × 1.8 cm, lobed 4/5 to costule basally, most pinnules 4–9 mm broad with rounded apex. Sori medial, indusia minute, pale brown, completely concealed by mature sporangia, sporangial stalks dark reddish-brown basally, paraphyses none.

MINDANAO. Bukidnon, Mt Dumalucpihan, June-July 1920, *Ramos & Edaño BS 39031* (US).

Ecology: Terrestrial.

Notes: Rosenstock described this species from Sumatra as exindusiate and an isotype in NY is indeed without indusia. However, specimens from Thailand, S. Japan, the Philippines, and Papua clearly have very small indusia. In Fern Fl. Philip. 2 (1960) 283, Copeland cited the one Philippine specimen as an unnamed relative of *D. sparsa.*

Distribution: Thailand and Sumatra to S. Japan and Papua New Guinea.

7. **Dryopteris sparsa** (Don) O. Ktze., Rev. Gen. Pl. 2 (1891) 813; Christ, Philip. J. Sci. 2C (1907) 213; Merrill, Philip. J. Sci. 3C (1908) 390; Copel., Leafl. Philip. Bot. 2 (1908) 389; Fern Fl. Philip. 2 (1960) 283; Holttum, Ferns of Malaya (1955) 492, t. 292; Hatusima, Mem. Fac. Agr. Kagoshima Univ. 5 (1966) 22. —— *Nephrodium sparsum* Don, Prod. Fl. Nepal. (1825) 6; Copel., Polyp. Philip. (1905) 24. —— *Aspidium sparsum* (Don) Spreng.; Christ, Bull. Herb. Boiss. 6 (1898) 194.

BATAN ISLAND. Mt Iraya, *Hatusima & Sato 29055* (PNH).

LUZON. Banawe, *Banlugan PNH 72907;* Mt Ugo, *Ramos BS 5836* (MICH, US); Mt Santo Tomas, *Price 1042, 1840;* Baguio, *Price 1578, Topping 222* (GH, US), *282* (MICH, US); Twin Peaks, *Bartsch 211* (US); Benguet, *Merrill 7779* (MICH, US); Mt Arayat, *Loher 1190* (US); Mt Banahaw, *Price 362*; Mt San Cristobal, *Price 804, 813, 839;* Mt Makiling, *Price 211, 366, 499, 2398.*

NEGROS. Mt Cuernos de Negros, *Elmer 9949* (F), *10100* (MICH), *Herre 1101* (NY), *Price 2612.*

PALAWAN. *Foxworthy BS 672* (MICH).

MINDANAO. Lanao, *Clemens s.n.* July 1907 (F); Zamboanga, San Ramon, *Copeland 1727* (MICH, US); Bukidnon, Mt Camates, *Ramos & Edaño BS 38607* (US); Davao, Mt Apo, *Williams 2526* (NY).

Ecology: Terrestrial in mountain forests, 800-2100 m, descending to 400 m in everwet ravines at base of Mt Banahaw.

Notes: Occasional specimens have globular sessile yellow glands on the lower laminar surface, a character possibly controlled by a single allele. Examples are: *Herre 1101, Price 813, 1578, 2398. Price 1042* from high elevation on Mt Santo Tomas has maroon stipe and rachis. Similar plants have been named *D. sparsa* var. *nitidula* (Bedd.) Ching, Bull. Fan Mem. Inst. Biol. Bot. 8 (1938) 472.

Distribution: Sri Lanka & India to S. Japan and Papua New Guinea.

8. **Dryopteris uropinna** Price, **sp. nov.** —— *Aspidium erythrosorum* auct. non Eaton: Christ, Bull. Herb. Boiss. 6 (1898) 193. —— *Nephrodium erythrosorum* auct. non (Eaton) Hook.: Copel., Polyp. Philip. (1905) 24. —— *D. erythrosora* auct. non (Eaton) 0. Ktze.: Christ, Philip. J. Sci. 2C (1907) 211;

Copel., Fern Fl. Philip. 2 (1960) 283. —— *D. subtriangularis* auct. non (Hope) C. Chr.: Ching, Bull. Fan Mem. Inst. Biol. Bot. 8 (1938) 485; Tard. & C. Chr., Fl. Gén. L'Indo-Chine 7 (1941) 315, fig. 35. —— *D. labordei* auct. non (Christ) C. Chr.: DeVol & Kuo, Fl. Taiw. 1 (1975) 377, p.p.

Fig. 1

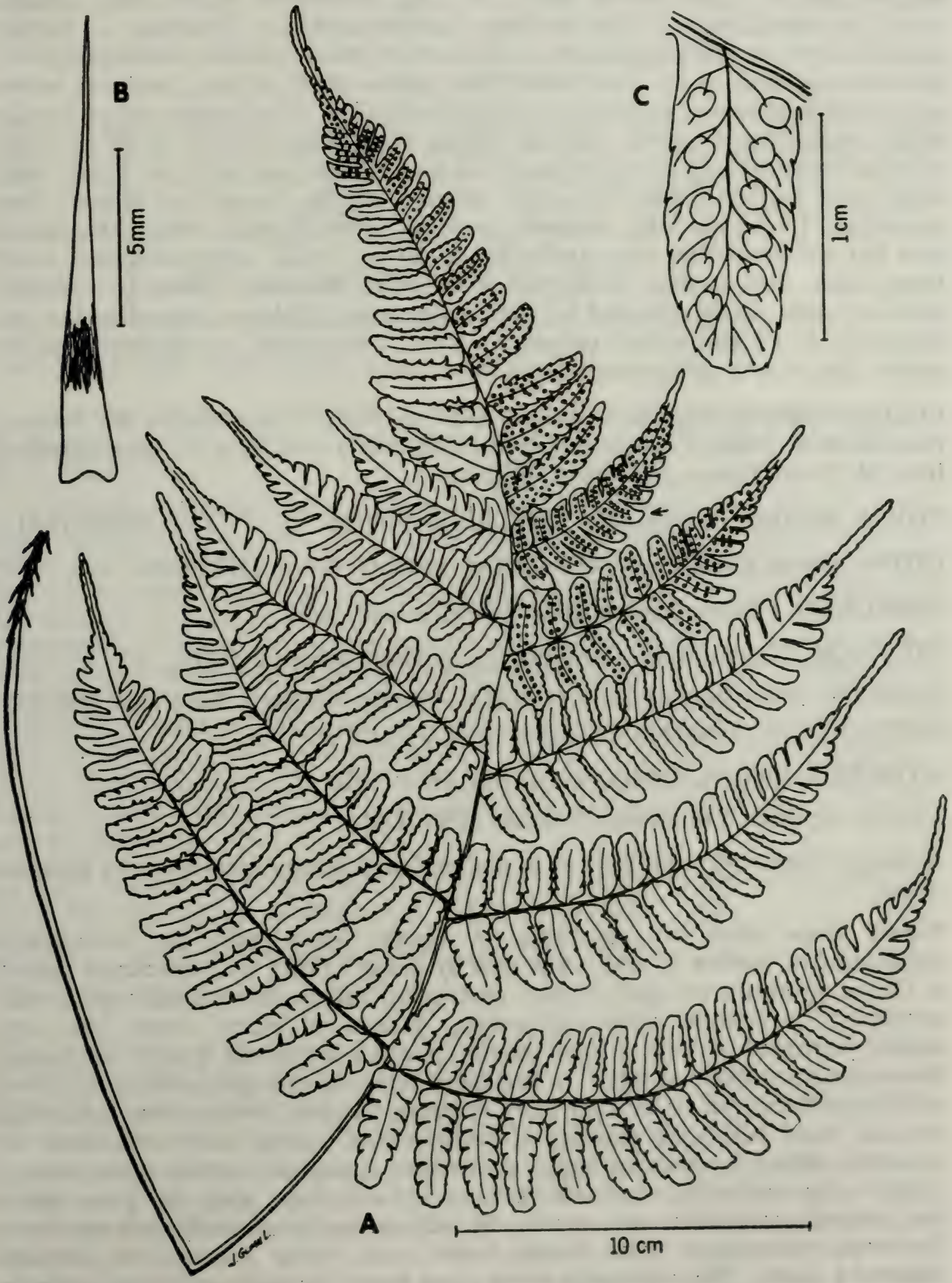

Fig. 1. *Dryopteris uropinna* Price, holotype. *A*. Frond. *B*. Stipe scale. *C*. Pinnule from upper pinna. (see arrow). Drawn by Ms. Janice Glimm Lacy.

Species e turma D. erythrosorae, ad D. indusiatam arcte accedens, differt magnitudine minore, ambitu subtriangulari, rhachidi glabrescenti, pinnulis late rotundati-truncatis, apicibus pinnarum frondisque abrupte contractis et caudatis.

HOLOTYPUS: Luzon, Ilocos Norte, Mt Burnay, *Price 3364* (MICH).

Rhizome short-erect, paleae c. 10 × 1 mm, linear, blackish with narrow brown margins, entire. Stipes brown, 14–34 cm long, glabrescent above base. Lamina deltoid to deltoid-ovate, 17–36 cm long, caudate-acuminate, bipinnate + deeply pinnatifid at base, thin papyraceous, dull brown or green, costae stramineous below, catadromous above base, above with a few narrow fibrils at axis junctions, below with small light brown bullate based acuminate paleae along costae and at costule bases, much-reduced septate hair-like paleae along veins. Pinnae to 16 cm long, broadest basiscopically, abruptly narrowed and caudate, on stalks to 4 mm long, basal pair longest; basal basiscopic pinnule slightly longer or shorter than succeeding, 1.5–4.1 cm long, shallowly to deeply lobed. Pinnules blunt, broadest at base but not auriculate, when undivided to 20 × 7 mm, with well-spaced small sharp teeth. Sori medial or slightly inframedial, indusium orbicular, centrally attached, sinus nearly obscured by overlapping edges, glabrous, shriveling but not deciduous, to 1.5 mm across, paraphyses short, non-capitate, on sporangial stalks, spores dark brown, rather irregularly tuberculate.

LUZON. Lepanto, Bagnen, *Copeland 1929* (MICH); Ilocos Norte, Mt Burnay, *Iwatsuki et al. P-849, Price 3364*. Christ (1898, 1907) also cited a Loher collection from Mt Santo Tomas, Feb. 1894, 2250 m.

CHINA. Kwangsi, *Ching 6263* (NY, US); Yunnan, *H. T. Tsai 60474* (GH).

INDIA. Assam, Khasi Hills, 4000 ft., Oct. 1890, *G. Mann* (NY, US).

THAILAND. Udawn, *Tagawa et al. T-645, T-1297* (US).

VIETNAM. Cochin-China, *Cavalerie s.n.* ex Herb. Jeanpert (US).

TAIWAN. Taito, *Tagawa 2670* (MICH); Agyoku, Taihoku, *Suzuki 24* (MICH).
OKINAWA. Mt Yonahadake, *Hatusima 18371* (US).

RYUKYUS. Ishigaki, *Koidzumi, s.n.* July 1923 (US).

JAPAN. Kyushu, Yakushima, *Iwatsuki 3159* (US).

Ecology: Terrestrial, 1800-2250 m in sheltered well-lighted spots in moist montane forest.

Notes: Hope cited two specimens of Gustav Mann with his *Nephrodium subtriangulare*, neither of which was seen by Ching (1938) who mistakenly named a Clarke specimen as type. Hope's description differs from Ching's plant (*D. uropinna*) by rhizome scales castaneous, "pinnae all except lowest pair very slightly narrowed at base, lowest inferior pinnules on lowest pinnae very much shorter than next three or four." In Philippine literature this species has been known as *D. erythrosora* which however has a creeping rhizome, brown paleae, and much reduced basal basiscopic pinnules of basal pinnae, among other differences. *D. indusiata* differs by attaining larger dimensions, lanceolate outline, more strongly paleate stipe and rachis, segments narrower apically, frond apex and pinna apices not suddenly contracted and caudate. *D. labordei* has prominently enlarged basal basiscopic pinnules of basal pinnae, brown (not black) paleae, and gradually narrowed apices. The specimens above cited from Thailand and Japan differ in minor respects from the Philippine type. Some Japanese specimens appear to intergrade with *D. indusiata;* they may be hybrids. Another similar species is represented by *Topping 1794* (US) from Mt Kinabalu; it differs by bullate scales absent, segments hardly toothed, basal basiscopic pinnule not dissected.

Distribution: Himalayan region to S. Japan and Luzon.

9. **Dryopteris varia** (L.) O. Ktze., Rev. Gen. Pl. 2 (1891) 814; Ching, Bull. Fan Mem. Inst. Biol. Bot. 8 (1938) 490; Copel., Fern Fl. Philip. 2 (1960) 284. —— *Polypodium varium* L., Sp. Pl. 2 (1753) 1090. —— *Aspidium varium* (L.) Sw.; Christ, Bull. Herb. Boiss. 6 (1898) 192; ibid. II, 6 (1906) 996. —— *Polystichum varium* (L.) Presl; Copel., Polyp. Philip. (1905) 18.

LUZON. Bontoc, *Madulid et al. PNH 113264, Vanoverbergh 624* (MICH); Ilocos Norte, *Iwatsuki et al. P-202, P-225, P-886, Price 3342, 3398;* Baguio, *Copeland 1959* (MICH), *Elmer 6489* (MICH, NY, US), *Hernaez CAHUP 13899, 13900, 13901, Price 386, 1677, Ramos BS 5795* (MICH, US), *Topping 177* (US), *Williams 1513* (NY, US); Mt Banahaw, *Price 882.*

Ecology: Terrestrial in seasonally dry forest, 700–1500 m.

Notes: The Banahaw collection is a new southern range extension.

Distribution: N.E. India, China, Korea, Japan.

10. **Dryopteris formosana** (Christ) C. Chr., Ind. Fil. (1905) 266; DeVol & Kuo, Fl. Taiwan 1 (1975) 376. —— *Aspidium formosanum* Christ, Bull. Herb. Boiss. II, 4 (1904) 615.

Rhizome short-erect, paleae fuscous, concolorous, subentire, to 20 × 2.5 mm. Stipes stramineous to brown, to 49 cm long, 6 mm thick at base, paleae blackish, entire. Lamina deltoid or deltoid-ovate, to 42 cm long, fully tripinnate at base, firm papyraceous, greyish-green, anadromous at proximal base, elsewhere catadromous. Rachis with reduced narrow blackish paleae, grooves with conical hairs at junctions, pinna-rachises, costae, and costules with small dark acuminate bullate-based paleae beneath, veins beneath with appressed multiseptate hairs. Basal pinnae to 19 cm long, stalk 9 mm, basal basiscopic pinnule notably enlarged, to 13 cm, secondary pinnules to 3.5 × 1.1 cm, tertiary pinnules to 8 × 3.5 mm, adnate, minutely aristate; basal acroscopic pinnule to 3.2 × 1.7 cm. Middle pinnae c. 13 cm long, acuminate, pinnules to 3.4 cm long, secondary pinnules adnate or confluent, aristate-denticulate. Sori about medial, indusium bright brown, to 1.3 mm across, glabrescent.

LUZON. Benguet Prov., Mt Santo Tomas. *Price 1117;* Ilocos Norte Prov., Solsona, *Price 2929,* Mt Burnay, *Iwatsuki et al. P-851, Price 3384.*

Ecology: Terrestrial in mountain forest, 1400-2100 m.

Distribution: Taiwan, Japan.

11. **Dryopteris subarborea** (Bak.) C. Chr., Ind. Fil. (1905) 295; Holttum, Ferns of Malaya (1955) 491, t. 291; Copel., Fern Fl. Philip. 2 (1960) 284, p.p. —— *Polypodium subarboreum* Bak., J. Linn. Soc. Bot. 24 (1887) 259. —— *D. purpurascens* auct. non (Bl.) Christ: Christ, Philip. J. Sci. 2C (1907) 213.

Rhizome short-creeping, c. 2.5 cm thick, paleae to 20 × 2 mm, brown, concolorous, with marginal projections from one or two adjoining cells bearing a small globose pale deciduous gland. Stipe stramineous, sparsely paleate, to at least 55 cm long, 12 mm thick at base, with c. 12 vascular bundles forming a single ring interrupted by the adaxial groove. Lamina to at least 110 cm long, ovate, to fully quadripinnate basally, anadromous throughout or nearly so, thin papyraceous, rachis with a few scattered appressed remnants of paleae, rachis groove, pinna-rachis grooves, and basal portion of pinnule grooves with minute erect capitate glandular hairs within, lamina otherwise glabrous. Basal pinnae to 60 cm long, stalk 1.5 cm to basal pinnule, apex acuminate, pinnules to 17 cm long, acuminate, secondary pinnules to 4.5 × 1.6 cm, blunt or acute, the proximal pinnate or lobed with rounded undulate-toothed segments, grading distally to shallowly crenate-dentate. Middle pinnae c. 32 cm long, acuminate, stalk 1 cm, basal pinnules 7.5 × 3 cm, secondary pinnules to 1.6 × 0.9 cm. Sori medial to slightly supramedial, indusium brown, glabrous, smaller than sorus, 0.5 mm across, paraphyses with hyaline or yellow bead-shaped heads.

LUZON. Quezon, Real. Llavac, *Price 1494, 1499;* Laguna, Mt San Cristobal, *Copeland PPE 91* (GH, MICH); Mt Makiling, *Elmer 18067* (F, GH, NY), *Price 2988.*

MINDORO. Mt Halcon, *Merrill 6101* (MICH)?

CATANDUANES. *Ramos BS 30192* (US), *30223* (US), *30462* (US).

SAMAR. Gandara, *Price & Hernaez 158.*

PANAY. Capiz, Mt Bulilao, *Martelino & Edaño BS 35645* (US), *35652* (US), *35693* (US), *35730* (US).

Ecology: Epiphytic on trunks and large branches in wet forest, 300–1200 m.

Notes: I place here with doubt *Merrill 6101* known to me by a single sterile specimen pustular beneath. According to the field label, a Bornean specimen at Kew, matching the type, was also epiphytic with short-creeping rhizome (R. E. Holttum, in litt.). Related is the New Guinean *D. pseudoparasitica* v.A.v.R. with relatively slender and long-creeping rhizome and dimorphic fronds.

Distribution: Sumatra, Malaya, Borneo (Java?).

12. **Dryopteris purpurascens** (Bl.) Christ, Philip. J. Sci. 2C (1907) 213, nomen tantum; Copel., Leafl. Philip. Bot. 3 (1910) 807; Backer & Posthumus, Varenflora voor Java (1939) 47, p.p. —— *Aspidium purpurascens* Bl., Enum. Pl. Jav. (1828) 169. —— *Nephrodium divisum* auct. non Hook.: Copel., Polyp. Philip. (1905) 26. —— *D. subarborea* auct. non (Bak.) C. Chr.: Christ, Philip. J. Sci. 2C (1907) 214, p.p.; Copel., Leafl. Philip. Bot. 3 (1910) 807; Fern Fl. Philip. 2 (1960) 284, p.p.

MINDANAO. Mt Apo, *Copeland 1138* (MICH, NY, US), *1614a* (MICH), *s.n.* 5 Sept. 1932 (MICH), *Elmer 11418* (MICH), *11550* (F, GH, MICH, NY, US), *11842* (F, GH, MICH, NY, US), *Williams 2479* (NY, US); Mt Matutum, *Copeland s.n.* 30 April 1917 (MICH), *Ramos & Edaño BS 85302* (GH).

Ecology: Terrestrial, petrophytic, or epiphytic on mossy trunks, 1500–2000 m.

Notes: *Elmer 11842* has a different appearance because of maroon color when dry and finer teeth of segments; it may represent another species. Mindanao specimens which I am treating as *D. purpurascens* differ from the next species, *D. permagna,* by being somewhat laxer and less dissected with broader usually deltoid teeth and inconsistently catadromous or anadromous architecture, as well as the paraphyses. The holotype of *Aspidium purpurascens* Bl. (photo MICH, US, Morton neg. 1304) consists of two separate pinnae evidently from the same frond. labeled as collected in the Moluccas by Zippelius. Blume's variety Beta (photo MICH, US, Morton neg. 1305) seems to be identical, possibly parts of the very same frond, consisting of a frond apex and the basal portion of a basal pinna, but is labeled Java, collector Blume. Both are quadripinnate, and anadromous throughout. While no Philippine materials are an exact match to the type of *D. purpurascens*, I refrain from describing the Mindanao plant as new without further information. Among other subtle differences, Javan plants have relatively numerous persistent narrow paleae along axes below.

Distribution: Java, Celebes, Moluccas (Borneo?).

13. **Dryopteris permagna** Price, **sp. nov.** —— *D. subarborea* auct. non (Bak.) C. Chr.: Christ, Philip. J. Sci. 2C (1907) 214, p.p.; Copel., Fern Fl. Philip. 2 (1960) 284, p.p.

Rhizoma crassum, erectum, paleis usque ad 42 × 7 mm cellulis marginalibus aliquot eminentibus ferens. Stipites usque ad 103 × 1.2 cm. Lamina subquinquepinnata, ovata, usque ad 138 cm longa, herbacea. Pinnulae primariae pleraque in positione catadromica portatae. Pinnae basales amplissimae, usque ad 64 cm longae, petiolus usque ad 10 cm longis, pinnula basali basiscopici usque ad 31.5 cm longa. Pinnulae ultimae apice rotundatae denticulatae, lateribus lobatae vel dentatae, lobis acutis erectopatentibus usque fere patentibus. Costae, costulae venaeque infra pilis persistentibus multiseptatis appressis praeditae. Sori medialis, indusia 0.5–1 mm diametro, glabra. Paraphyses inconspicuae, hyalinae, non capitatae.

HOLOTYPUS: Luzon, Mt Santo Tomas, *Price 1611* (PNH).

Rhizome stout, erect. Paleae to 42 × 7 mm, long-acuminate above a relatively broad lower portion, brown, concolorous, margins with small blunt projections consisting of the outcurved portion of one cell or two adjacent cells. Stipe light brown, with smaller narrower paleae, to 103 cm long and 12 mm thick, with 15 vascular bundles near base, the two adaxial on either side of the stipe-groove much the largest. Lamina ovate, to 138 cm long, olive-green, herbaceous, quadripinnate or subquinquepinnate at base, pinnae and major pinnules long acuminate, most or all pinnae with basal primary pinnules in catadromic position, secondary pinnules in anadromic position except sometimes for the larger ones of basal pinnae, tertiary pinnules and quaternary segments nearly all in anadromic position. Major axes beneath with deciduous narrow fibrils, persistent appressed reddish-brown multiseptate hairs c. 0.3 mm long borne along costae, costules and veins beneath, sometimes a few on upper surface. Basal pinnae largest, to 64 cm long on stalks to 10 cm long, basal basiscopic pinnule to 31.5 cm, stalk to 1.8 cm, not very much larger than the succeeding, basal acroscopic pinnule to 20.5 cm, very slightly shorter than the several succeeding. Largest secondary pinnule 10 cm long, tertiary pinnules to 2.5 × 1.7 cm, largest quaternary pinnules broadly adnate or connate, to 10 × 5 mm. Third pair of pinnae from base 45 cm long, fifth pair 33 cm long with stalk 2 cm, tenth pair 12 cm long, ultimate pinnules with broad blunt denticulate apices and spreading-ascending pointed lobes or teeth. Sori about medial, indusia 0.5–1 mm across, brown, glabrous, paraphyses shorter than sporangia, apices hyaline, not or hardly expanded.

LUZON. Mt Polis, *Oliver PNH 30576;* Mt Data, *Ramos & Edaño BS 40285* (US); Mt Pauai, *Sulit PNH 5120* (MICH); Bontoc, *Ramos & Edaño BS 37834* (US), *37847* (US), *37985* (US), *38064* (US); Mt Ugo, *Ramos BS 5777* (MICH, NY, US); Haight's Place, *Mearns BS 4194* (MICH, US); Baguio, *Loher 832* (US); Mt Santo Tomas, *Price 1611, 1862*.

Ecology: Terrestrial in mountain forest, 1400–2200 m.

Notes: *Ramos & Edaño BS 37847*, very congested and nearly glabrous, is placed here with some doubt. This species, apparently endemic to Luzon, is very similar to Polynesian specimens of *D. arborescens* (Bak.) O. Ktze., which is characterized by broad pale brown paleae on costae, the paleae attached parallel to the costa.

Another similar Polynesian plant, *D. maxima* (Bak.) C. Chr., is anadromous, very finely dissected, with supramedial sori. Some New Guinean specimens are similar to those of Polynesia; none are quite the same as anything in the Philippines.

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Fertile-sterile Leaf Dimorphy in Ferns

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In addition to his many other contributions, Dr. R. E. Holttum has been unquestionably one of the world's leading authorities on the taxonomy of ferns with fertile-sterile leaf dimorphy, especially the lomariopsid group. Inspired in part by reading his papers, we became interested several years ago in the over-all subject of fertile-sterile dimorphy and began the study to be reported here. As will be seen, there are numerous disagreements in the interpretations of dimorphy, and this represents an effort to review these as well as other aspects of the general phenomenon.

Dimorphy of fertile and sterile fronds is widespread and bears upon both the systematics and ecology of ferns. It is an expression of a trend found throughout vascular plants, a trend which achieves its ultimate in seed plants. Recognizing that the term "dimorphy" may sometimes apply to other than fertile-sterile (i.e., various types of heterophylly of vegetative leaves in ferns), for convenience the term here will be confined to differentiation into sporophylls (spore-producing fronds, *fertile Blätter*) and trophophylls (purely photosynthetic fronds, *Laubblätter*). Profound alterations may appear in the evolutionary transition from primitive monomorphy, including transformations in morphology, anatomy, physiology, and ecology. These changes are thought to possess adaptive value. However, this idea is not universally accepted, and there is little or no experimental evidence to support it. At present, in fact, most of our conclusions are intuitive and hypothetical, and we strongly need rigorous tests. We hope that the ideas we present here will help to stimulate such experimentation.

As many as one in five of all fern species possess what may be called fertile-sterile dimorphy, but this figure has to be arbitrary because of so many transitions that occur between monomorphy and dimorphy. Where the dimorphic condition is strongly expressed, taxonomists have traditionally utilized it as a useful character in species discrimination. In some instances, taxonomic separations have been created even at the generic level on the basis of sporophyll-trophophyll dimorphy.

The analysis of foliar dimorphy invokes a multitude of biological questions such as what parts undergo changes, what are the effects on sporangial arrangement, what developmental processes underlie formation and timing of fertile expressions, what — if any — ecological advantages are conferred, and to what extent dimorphism is valid as a systematic character. The following report is an outcome of our observations in the field, laboratory, and herbarium, together with a survey of the literature. The most thorough and most recent survey seems to be that of F. G. Dickason in 1946. Because of the widely scattered nature of references to this subject, we fully expect that some important items have been overlooked. We also anticipate that various ideas expressed here will be subjected to future

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reappraisal. If, however, this article serves to stimulate critical research, its purpose would be fulfilled.

All degrees of morphological and anatomical divergence exist between fertile and sterile fronds. In fact, one of the reasons the term "monomorphic" is rarely used may be that practically all ferns are strictly speaking at least slightly dimorphic. Steps in dimorphic divergence are well exemplified in numerous genera. In eastern North America, for example, we encounter a good illustration in the woodfern genus, *Dryopteris*. *D. goldiana* (Hook.) Gray has hardly any detectable difference between soriferous and non-soriferous mature fronds. *D. cristata* (L.) Gray, with erect, tall fertile fronds, and spreading, short sterile fronds, shows strong differentiation. *D. spinulosa* (O. F. Muell.) Watt is intermediate. Other good examples of such sequences are met with over a broad taxonomic spectrum, such as, in Polypodioideae, *Loxogramme*, *Microgramma*, and *Pyrrosia;* in Blechnoideae, *Blechnum;* and in Dryopteridoideae, *Davallia*, *Humata*, *Nephrolepis*, *Oleandra*, and *Polystichum*[2].

It should be understood that the term "dimorphism" does not necessarily imply a precise morphological parallelism. The changes involved are probably often the result of analogous, rather than homologous, transformations, and different examples show different degrees of involvement of petioles, blades, pinnae, sporangial arrangements, histology, and physiological reactions.

The sporophyll-trophophyll differentiation may embrace whole fronds or only parts of fronds, and in the latter, it may be the tip that is fertile, the middle of the frond, or the base. These modifications are diagrammed in Figure 1. Interfoliar dimorphy, constituting complete differentiation of whole fronds is the most common type. However, because of the commonly transitional nature of the manifestations, many fertile fronds are merely "subdimorphic" (term as used by Dickason, 1946) in the sense that the changes displayed are incomplete in kinds and amounts. A "holodimorphic" situation includes total loss of vegetative function in the sporophyll. However, the latter is hard to achieve because during the early stages of maturation the rachises and costae of all fertile fronds (at least those known to us) are to some extent green and photosynthetic. Whole-frond differentiation into sporophylls may follow two routes. It may be the culmination of an evolutionary trend in which at first only the frond tip is fertile. Dickason (1946) suggests that there is a progressively earlier shift from the vegetative to the reproduction condition of the leaf starting at the apex (i.e., Fig. 1, B to D) mediated by an hypothetical "sporogen" growth substance. On the contrary, one can just as well imagine modification of the whole leaf progressing from the inception of the leaf, bottom to top.

Where fertile-sterile differentiation appears in separate parts of the same leaf, "the term *hemidimorphism* is used instead of *dimorphism*" (Dickason, 1946). The hemidimorphic leaves with terminal fertile pinnae are the most widespread. In Osmundaceae, this condition is illustrated by the familiar *O. regalis* L.; in Polypodioideae, by the genera *Paltonium* and especially *Belvisia*; in Grammitidoideae, by *Grammitis* Sect. *Xiphopteris;* and in Adiantoideae, by *Llavea*. Two extremes in the Dryopteridoideae are observed in the eastern North American *Polystichum acrostichoides* (Michx.) Schott and *Dryopteris ludoviciana* (Kze.) Small. As in other forms of hemidimorphism, the fertile pinnae —— even when they are photosynthetic at the time of spore production as they are in *D. ludoviciana* —— are shorter-lived than the sterile, and turn brown and die well before the sterile pinnae.

Examples of hemidimorphism in which only the medial pinnae are the fertile ones are known best in *Osmunda*, and most familiarly in *O. claytoniana* L.. which is designated in North America by the colloquial name of "interrupted fern"

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[2] The family-subfamily classification used in this paper is that of W. Wagner (1973).

because its fertile pinnae discharge their spores and fall off early in the season (usually by early or middle July), leaving fronds in which the lower and upper regions of photosynthetic pinnae are set apart by a length of naked rachis.

Ferns with the hemidimorphic condition effecting only basal pinnae are taxonomically a motley lot. In the striking cyatheoid genus *Thyrsopteris*, known in the living flora only from Juan Fernandez Islands, several pairs of lower pinnae are fertile, these extremely skeletonized (i.e., lacking lamina) but bearing sori with conspicuous cup-like indusia. More abundant ferns with modified basal pinnae occur in Ophioglossaceae and Schizaeaceae subg. Anemioideae. In the genus *Anemia* we find a spectrum running from only subtly subdimorphic basal pinnae all the way to fully differentiated basal pinnae. Accompanying this progressive laminar reduction and skeletonization of the basal pinnae pair, there is increased tendency for them to become erect and tower above the spreading sterile pinnae. In the most evolved forms in *Anemia*, the sporangial masses are held well above the photosynthetic portions of the leaves, and effectively the same result is achieved as in those dimorphic leaves in which the sterile fronds are flat and form rosettes (cf. Fig. 1, C, hemidimorphic, with Fig. 2, D, holodimorphic). The alterations in *Anemia* have been described in some detail by Mickel (1962, 1967). One of the interesting features in specialized members of this genus is the close association of the fertile basal pinnae in point of apparent origin with the second pair of pinnae, i.e., the lowest of the sterile pinnae, a condition to which Mickel refers as "fertile pinnae approximate to sterile." On the basis of comparative morphology, we can conclude that the fertile petiolule bases have fused with the main petiole up to the first sterile petiolules. A parallel condition is seen in the single fertile spike of certain Ophioglossaceae, e.g. *Botrychium virginianum* (L.) Sw.

Mickel (1967) describes the probable evolution of the fully fertile fronds of certain species of *Anemia* as following a pathway opposite that suggested by Dickason (see above) for other holodimorphic ferns. Most *Anemia* taxa produce a single pair of fertile basal pinnae, but in *A. rutifolia* Mart. there is more than one pair of basal fertile pinnae, and in *A. millefolia* Gardn. all of the pinnae are fertile. We do not believe that the two models are necessarily in conflict, nor the idea, suggested earlier, that in some cases the sporophyll may have been holodimorphic from the beginning. There are thus three different possible routes: (*a*) change directly from monomorphic leaves to holodimorphic (Fig. 1, A-D); (*b*) change from monomorphic to hemidimorphic, with the fertile pinnae apical, to holodimorphic (Fig. 1, A-B.D); and (*c*) from monomorphic to hemidimorphic with the fertile pinnae basal to holodimorphic (Fig. 1, A-C-D). Monographers should be prepared to encounter any one of these routes in a given evolutionary line.

Morphologically the single fertile spike of Ophioglossaceae (*Botrychium, Helminthostachys, Ophioglossum*) resembles the fertile basal pinna condition in *Anemia*, differing from it in the apparent fusion to form a single primordium and mature structure. This interpretation —— the "Fusion Theory" or "Peltation Theory" —— to explain the fertile spike, is the most parsimonious and requires the least number of assumptions [3]. Unfortunately, the morphological intermediates that would directly confirm the phylogeny of the fertile spike have been lost from the fossil record. All we have are data from living forms to support this interpretation —— the pattern and origin of vascular strands, and the occasional grapefern specimens (especially in *Botrychium* subg. *Sceptridium*, considered primitive on other grounds) of the *Anemia* condition with separate fertile basal pinna pairs, as

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[3] In the welter of interpretations to which the fertile segment of Ophioglossaceae has been subjected, one of the most unusual is that of Wieffering (1964), who, regarding Ophioglossum, treats the sterile segment of the frond as a "trophophyll' and the fertile spike as comprising a "fertile stalk" terminated by a "strobilus"!

well as intermediates. There are a few examples of adder's-tongue ferns, *Ophioglossum,* with the sterile blade reduced or suppressed entirely. However, the belief that the rare South African species, *O. bergianum* Schlecht. has complete sporophyll-trophophyll separation (as believed, for example, by Copeland, who keyed it out on this basis in 1947) has proved to be erroneous. In our own observations of this curious plant we find an illusion of two separate fronds that is created by a very low attachment of the fertile spike to the sterile segment.

Although the details are not agreed upon, the consensus seems to be that the sporocarps of the Marsileaceae are modified basal pinnae in which the sporangia are encapsulated. Unless it can be established that the sporocarps are *de novo* in origin, comparative morphology dictates that the homology to basal pinnae is the most likely explanation of these very distinctive structures, especially if it is agreed that Marsileaceae are specialized leptosporangiate ferns. Gupta (1956, 1962) has brought together much of the information bearing upon the nature of the sporocarp. Also, he has found (pers. comm.) very interesting forms of *Marsilea minuta* L. which have numerous sterile pinnae borne along the leaf axis, suggesting a reversal to a more primitive condition. It is easy to speculate that the hemidimorphic condition of Marsileaceae may have more than a coincidental resemblance to that of the Anemioideae.

Attention should be called to the less spectacular but substantial changes that often occur in the specialization of distinct trophophylls. The obviously striking aspect of many sporophylls quickly attracts attention from morphologists and taxonomists, but often the trophophylls themselves do not remain merely as sterile remnants but little changed from the original double-duty leaves of the monomorphic ancestors. The uncommon curly-grass fern, *Schizaea pusilla* Pursh, of northeastern North America has trophophylls which are wiry, twisted organs concentrated at the base of the plant. In various polypodioid genera, such as *Microgramma* in the New World and *Pyrrosia* in the Old, there seems to be an inverse correlation between changes in the sporophyll and those in the trophophyll: As the sporophyll becomes longer and narrower, the trophophyll becomes shorter and wider. Holttum (1954) illustrates *Pyrrosia nummularifolia* (Sw.) Ching, an extreme example in its genus with the sterile fronds "very shortly stalked, almost circular to broadly ovate." In this example, the fertile fronds are more similar to the norm of the non-dimorphic or subdimorphic fronds of the genus than are the sterile. Figure 2, D, illustrates this type of change in trophophylls.

In a few of the paddle-ferns, *Elaphoglossum,* the trend described above is reversed: The trophophylls become linear, extremely long and narrow, and pendent, while the sporophylls retain their lanceolate outlines. Splendid illustrations of such specialized hanging trophophylls are the New World tropical *Elaphoglossum siliquoides* (Jenm.) C. Chr. and especially *E. herminieri* Bory ex Fée.

In teleological terms, the "need" for certain leaf shapes required by carrying out both duties of photosynthesis and sporulation seems to be eliminated if sporophylls evolve, permitting the trophophyll to become more adapted to its role. In *Dryopteris cristata,* the sterile leaves are smaller and more spreading, so that they form a "light-catching" rosette at the base of the plant in contrast to the bulk of the species of *Dryopteris* in which the sterile fronds are less differentiated from the soriferous fronds. In general, in terrestrial forms, the flatter and rounder the trophophyll, the more efficient it will be photosynthetically. This seems to be true also in those epiphytic ferns, such as the creeping polypodioids, in which the trophophylls "hug" the branches and twigs of the host trees and shrubs.

A somewhat neglected component of comparative morphology of the sporophyll is the modification of sporangial distribution. The over-all trend is toward the concentration of sporangia, but this concentration is achieved in a variety of ways. The sori may keep their organization and simply become more tightly grouped.

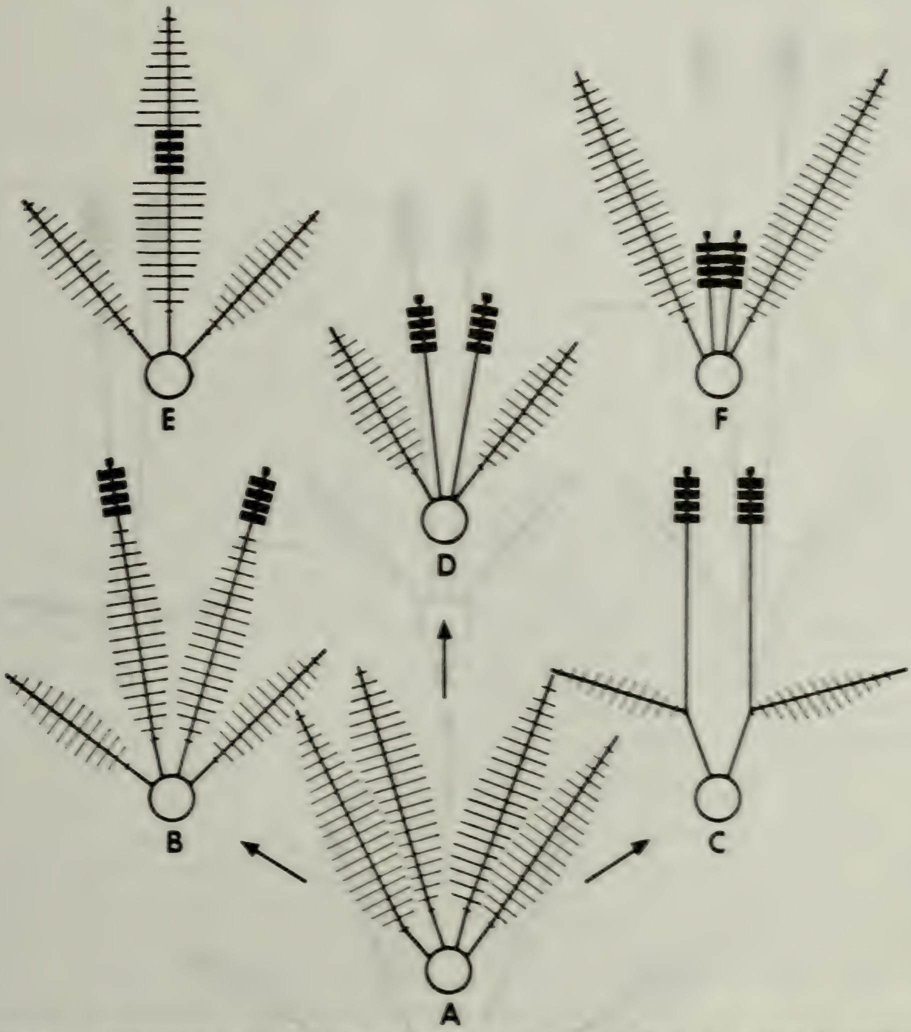

Figure 1. Diagrammatic representation of fertile-sterile dimorphy. *A*. Primitive condition: monomorphic. *D, F*. Complete dimorphism of sporophyll and trophophyll, showing different relative sizes of sporophylls. *B, C, E*. Hemidimorphic conditions: *B*. Fertile parts terminal. *E*. Fertile parts medial. *C*. Fertile parts basal.

They may, on the other hand, lose their soral organization and fuse into a continuous "sheet" of sporangia spread over the sporophyll lamina, or the entire sporangial area may become skeletonized, losing laminar webbing completely and producing clusters of single-veined axes. The sporangia may be exposed, even in the youngest stages of development (as in certain acrostichoid ferns), or they may be protected by indusia, paraphyses, or by inrolling of laminar tissue to form more or less persistent sheltering capsules. Also, these various modifications may be combined in different ways.

Compacted but still discrete sori are observed in diverse taxonomic groups. The exposed epidermal areas between the sori are reduced so that finally no bare epidermis can be seen and the sori are in contact on all sides. For polypodioid sori this is well illustrated in the genus *Pyrrosia*. While it is true that after spore discharge members of this genus may appear to have truly acrostichoid soriation,

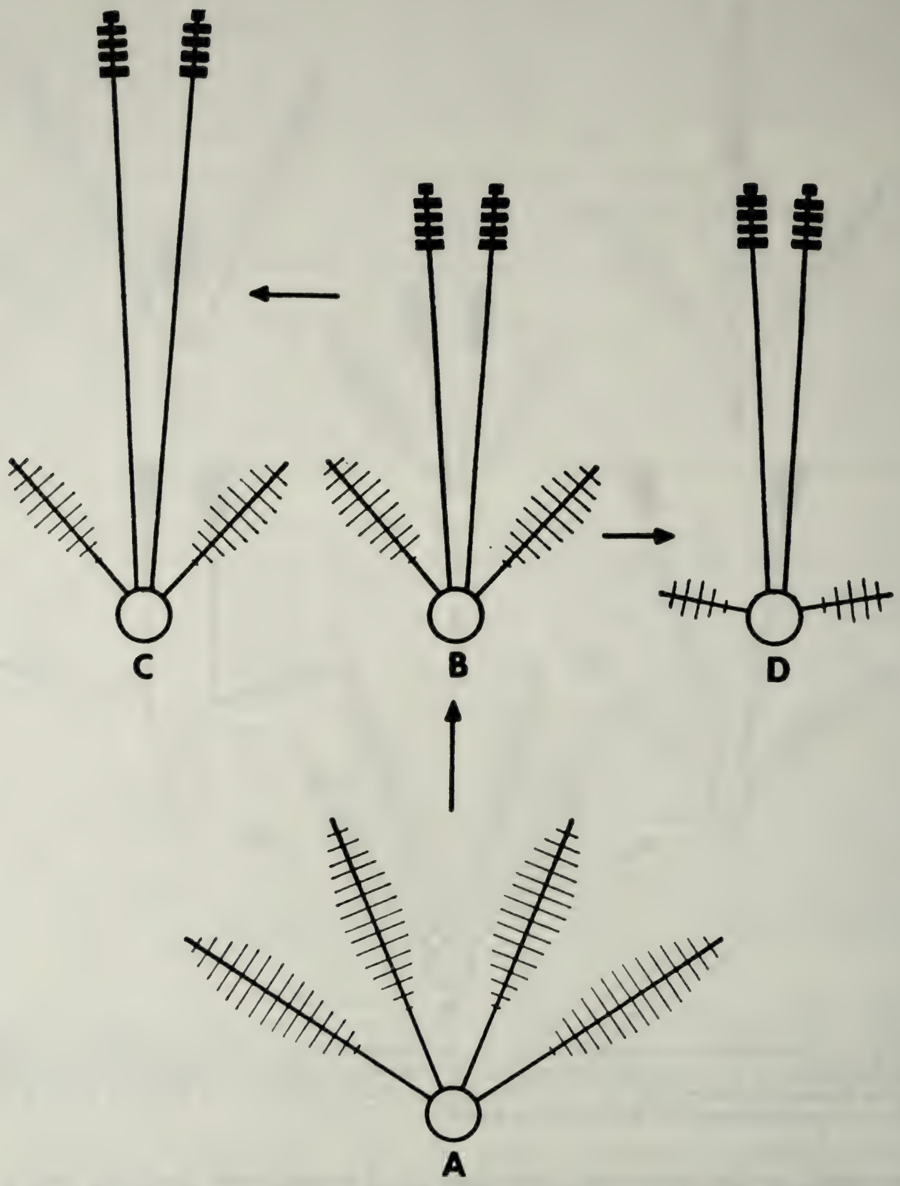

Figure 2. Diagrammatic representation of relative differentiation of sporophylls and trophophylls. *A*. Primitive condition: monomorphic. *B, C, D.* Dimorphic. *C.* Extreme change in sporophyll, the characters (height, orientation, exaggerated). *D.* Extreme change in trophophyll, specializations of size, shape, and orientation strong.

this is actually an illusion. Sori of the ancestors of *Pyrrosia* were probably of the type seen today in *Pleopeltis* —— well separated, exindusiate, and round. An outstanding example of nearly confluent indusiate sori is present in the eastern North American *Polystichum acrostichoides* (L.) Schott. Here the situation resembles that in *Pyrrosia* in that after spore discharge the fertile pinnae become falsely acrostichoid. Prior to spore discharge, however, not only are the discrete sori recognizable, but each is provided with a conspicuous peltate indusium.

Truly acrostichoid soriation results from the origin of sporangia upon a continuous placental surface which extends across the abaxial surface of the blade or pinna. Even in young stages it is not possible to make out individual sori. Although there are some disagreements over details of interpretation and terminology (cf. W. Wagner, 1965, pp. 299, 300), recognition of this type of soriation is generally accepted as a valuable tool in generic taxonomy. Ferns with acrostichoid soriation may or may not have laminar contraction associated with it. In *Elaphoglossum* (Aspleniaceae subg. Dryopteridoideae) and *Acrostichum* (Adiantaceae), the fertile blades or pinnae may be only slightly contracted or not contracted at all. However, they tend to be more ephemeral than the sterile blades or pinnae, becoming curled and dry before the sterile segments. Acrostichoid soriation in unrelated taxa probably has had different modes of origin. In *Acrostichum* the ancestors were very likely gymnogrammeoid ferns lacking indusia. The sori were linear and followed the veins, and they were separated by exposed laminar surface. By extension of the sori into the naked areas and finally becoming confluent, the acrostichoid condition came about, the sporangia making up a continuous sheet, clothing the entire laminar undersurface. On the contrary, the history of *Elaphoglossum* may have followed a very different route. If we accept the comparative evidence from many characters, *Elaphoglossum* is a derivative of ferns with round, indusiate sori (like those of *Dryopteris* and *Polystichum*). The steps in the evolution of *Elaphoglossum* from its probable progenitors may then be suggested to have followed this route: (1) assumption of the epiphytic habitat, (2) simplification of the frond, divided to undivided, (3) approximation of sori, from remote to continuous (as seen today in *Polystichum acrostichoides*), (4) loss of indusia, and (5) unification of placental tissue all across the laminar surface to become acrostichoid. Some of these steps may have taken place in a different order. The important point is that the acrostichoid condition may be the result of convergent evolution and not necessarily be a signal of systematic affinity. Surely the examples known in the polypodioid ferns (e.g., *Belvisia*, *Christiopteris*, *Dendroglossa*, and *Platycerium*) arose from very different ancestors from those given above.

Bower pointed out long ago (1923) that some acrostichoid ferns have "no special vascular provision for the nutrition of the sporangia", whereas others develop elaborate modifications involving two parallel vascular systems —— the normal venation plus a specialized receptacular venation on the abaxial side. The two are in connection with each other, of course. The state of having two parallel vascular systems is termed "diplodesmic", and is especially well shown by acrostichoid examples in the Polypodioideae (Bower, 1928).

What we here call the *botryoidal condition*, in which the sporangia form clusters upon more or less naked and branched axes, is best shown in three groups ——Ophioglossaceae, Schizaeaceae subg. Anemioideae, and Osmundaceae. Here the flat laminar condition is partially or entirely lost, and the sporangial masses become three-dimensional and glomerulate. Assuming that lamina-borne sporangia are ancestral (see discussion below) we may conclude that the primitive condition in Osmundaceae is that displayed by *Todea* and in Anemioideae by *Mohria* or certain members of *Anemia* itself. The only presumed primitive or intermediate conditions found in Ophioglossaceae are occasional forms or terata in which the sporangia are borne upon partly or fully developed lamina. This is especially well shown in certain species (e.g., *Botrychium matricariifolium* A. Br. and *B. simplex* E. Hitchc.) in which a percentage of every population shows sporangia arising from the sterile segment margins.

Sporophylls which have the *encapsulated* or *angiosporangial condition* are especially well developed in Plagiogyriaceae and Aspleniaceae subf. Blechnoideae. In these ferns the sporangia are covered, at least partially, by the inrolling of the pinna margins. They are protected until they are fully mature and ready to discharge the spores. To study early stages of sporangial development it is necessary to cut away or pull back the folded-over lamina. The most highly evolved encapsulated structures are those of the onocleoid ferns, especially *Matteuccia* and *Onoclea,* in which the sporophyll capsules do not open until months after the sporangia have matured.

Fertile-sterile differentiation at the histological level has been largely uninvestigated and we are currently trying to determine the scope of the anatomical changes associated with sporophylls. By using the frequent intermediates that occur as abnormalities in many dimorphic taxa, it is possible to detect gradients and establish homologies. Techniques of clearing and staining portions of the leaves are especially suited to this type of study. A brief summary of our observations is as follows: Narrowing of the segments of sporophylls is accomplished by the progressive reduction of the lamina until, in extreme cases like the botryoidal types described above, the axes become terete and there is no trace of laminar wings. Associated with this there is a large increase in the ratio of over-all surface to volume, allowing for more rapid drying. With reduction in lamina we usually notice an increase in the width of the vein intervals and a simplification of the vein pattern. The latter is accomplished by eliminating some of the vein branchings and most or all of the areoles, as in *Lorinseria areolata* (L.) Presl (Blechnoideae) and *Onoclea sensibilis* L. and *Onocleopsis hintonii* F. Ballard (Dryopteridoideae, Labouriau, 1958; Lloyd, 1971). In *Lomariopsis* the sporophylls have free-ending veins, lacking the marginal connections of the trophophylls (Holttum, 1939). Comparative investigations of the vein intervals of nearly two dozen taxa were made by Lommasson and Young (1971), but they did not compare conditions in sterile and fertile fronds.

There may be simplification in other laminar tissues as well. The epidermis may be softer in sporophylls than in trophophylls, and may tend to produce fewer stomates. The epidermal cells may be larger and straighter-walled. The mesophyll may have less elaborate spongy parenchyma that is composed of larger, thinner-walled cells. In most strongly dimorphic taxa, the cells lose their chlorophyll at maturity, appearing *en masse* a whitish, yellowish, or brownish color. Where the acrostichoid condition occurs, the sporangial initials are no longer localized in punctate or linear receptacles, but become spread over the abaxial surface, forming a continuous placental area both along and between the veins. As indicated earlier, the sporophyll venation of certain acrostichoid ferns may actually be more complex than that in the trophophylls.

The physiological study of sporophyll-trophophyll differentiation is still in its infancy. One thinks of such names as Labouriau, Sharma, Steeves, Sussex, Wardlaw, and Wetmore in connection with processes of initiation and development of fertile leaves. White (1971) has reviewed much of their work. There seems to be little question that formation of sporophylls is controlled hormonally, and that their timing is related to periods of light and perhaps heat, although there is a vast amount of research needed to clarify the factors involved. Various extraneous influences may interfere with the normal course of sporophyll development, causing intermediate fronds to form. There are scattered reports on effects of injuries brought on by such agents as fire, flood, mowing, destructive substances (e.g., tar), and the trauma of transplanting, in inducing intermediate fronds, but there are very few controlled experiments to warrant general conclusions. It does seem that destruction of many or all of the actively photosynthetic fronds of a given plant will have a tendency to produce imperfect expressions of sporophylls in the new crop of fronds. In *Polystichum acrostichoides,* the partially fertile, subdimorphic pinnae of "forma *incisum* (Gray) Gilbert" apparently result from abnormal new growth of late leaves after injury of the normal fronds of the season (Wagner, Farrar, and McAlpin, 1970).

In very strongly marked dimorphy, the fertile frond becomes less responsive to light and more responsive to gravity. The typical spreading orientation of the trophophyll in which the blade approaches a position perpendicular to the direction of light is absent in the sporophyll which is now so negatively geotropic that it becomes totally erect. A simple and quick experiment to demonstrate tropism of fertile parts may be made with *Botrychium virginianum* (L.) Sw. If whole leaves, including both the fertile and sterile segments, are cut off at ground level during the active growing season before the sporangia have fully matured or dicharged, and laid in pans of water in various positions, we have found that at room temperature in only 10 to 20 hours all of the fertile spikes will twist and become upright, no matter what the position of their associated sterile segments, illustrating dramatically the "urge" to raise the sporangia to the highest position possible.

The tissues of the sporophylls, being simpler than those of trophophylls and having a more flimsy structure, are more readily dried out. Their vertical position in relation to sun and wind, in contrast to the trophophylls which are closer to the substrate and more protected, also promotes dessication. Presumably the sporophylls have "cheaper construction" partly because they are more ephemeral and, lacking photosynthesis, have no value to the plant after their function of spore production is finished. Support by the rest of the plant is withdrawn when the sporophyll's job is done, and the fertile frond accordingly turns brown, dries out, and falls away. This is shown especially well in single hemidimorphic leaves. The differentiated fertile tips of *Osmunda regalis* and *Polystichum acrostichoides* dry up and die long before the sterile parts of the same leaf. In *Botrychium, Ophioglossum,* and *Anemia,* the photosynthetic pinnae continue to function as if nothing had happened, even though major parts of the leaf, the fertile segments, have collapsed and turned to twisted debris.

The seasonal timing of sporophylls and trophophylls may differ profoundly in taxa occurring in the same geographical areas and habitats. Nozu (1968) studied periodicity in Japan of members of nine genera with respect to sterile-fertile frond maturation, and reported that in a given species they may differ by as much as six months. Usually the sterile fronds mature first during the course of the year, but in *Osmunda japonica* Thunb. the fertile fronds mature a month or so earlier than the sterile.

A most curious state of affairs is found in the periodicity of *Botrychium lunarioides* (Michx.) Sw., a rarity of the southeastern United States known as "Winter Grapefern." The frond arises above ground in November and the sterile segment expands to its full size by sometime in January. The fertile segment, on the contrary, remains curled over at the ground level and stays soft and meristematic for nearly three months, only expanding and become erect in March. Spore discharge occurs in late March and then the entire leaf, including both fertile and sterile segments, dies in April. The plants are dormant, and completely buried under ground, from April to November.

Of what adaptive value is fertile-sterile leaf dimorphism? It is found in plants of such widely different habits and habitats that it is practically ubiquitous. The condition is found in giant ferns (e.g., *Acrostichum*) and midget ferns (e.g., *Peltapteris*), in thick-textured ferns (e.g., *Polystichum*) and thin-textured ones (e.g., *Trichomanes*). Dimorphy occurs in ferns with simple leaves (*Pyrrosia*) and with compound leaves (*Maxonia*). It exists in taxa that are terrestrial, taxa that are epiphytic and taxa that are aquatic. It is found in taxa with upright stems, with creeping stems, and with climbing stems. Xerophytes and hydrophytes, arctic and tropical ferns —— all have dimorphic representatives, the common species as well as the rare.

For what ecological reasons has dimorphic evolution occurred in such a gamut of ferns? One can, of course, ask the same question regarding other pteridophytes —— *Equisetopsida* and *Lycopodiopsida* —— which have made analogous changes of shoots rather than leaves. In all likelihood, similar forces have operated to produce strobili (analogous to apically hemidimorphous fronds) and whole fertile shoots (analogous to fertile-sterile segregation of whole fronds, for example *Equisetum arvense* L. and *Lycopodium carolinianum* L.).

Some major extrinsic factors to take into account are seasonality, radiant energy (e.g., heat, light), role of air and water, and biotic factors (e.g., shading, grazers, fungi). The plant functions of most importance here are photosynthesis, spore production, and spore dispersal and establishment.

All of the following adaptations may contribute to the differentiation of sterile and fertile fronds:

1. To elevate spores of the fertile fronds into the wind stream for maximum dispersal.
2. To permit more extreme drying effects to enable sporangia to open and close efficiently.
3. To spread out photosynthetic blades in horizontal positions for maximum reception of light.
4. To place photosynthetic blades in most humid surroundings to counteract water loss.
5. To bring photosynthetic blades closer to the substrate where there are higher carbon dioxide concentrations during day time.
6. To enable differentiation of seasonal timing for most favourable period for spore reproduction and most favourable period for vegetative assimilation.
7. To separate fertile from sterile parts if one or the other is more liable to grazing or fungal attack.

Most authors agree that sporophylls tend to bring the spores into a position where they can better be carried away by the wind. Holttum (1938) describes the common situation which "takes the form of a somewhat contracted lamina in the fertile fronds, which stand erect, on longer stipes than the broader sterile fronds which bend away in a rosette around them. ... This form of dimorphism undoubtedly helps the distribution of spores, raising the sporangia well above the surrounding leaves and exposing them to drier air and any slight wind that may exist."

Copeland (1906) emphasized the drying aspects in his analysis. In his words, "Dimorphism, whether merely begun, or highly developed, whether a character of whole fronds or of their parts, has in all cases the object of permitting the proper dryness of the mature sporangia without an improper desiccation of the vegetative structures. This is done by merely raising the reproductive structures farther above the substratum; or (rarely) by special structural devices, such as notched margins; by a restriction of the assimilating surface of the reproductive frond or region, so that it may be sacrificed in emergency; or by a more complete elimination of the vegetative structures in constitutionally ephemeral fertile fronds."

As already stressed, origin of sporophylls is accompanied often by increasing divergence or specialization of the trophophylls or trophophyllary blade parts. This specialization invokes progressive broadening of the blade together with reorientation into spreading or horizontal position. The blade becomes shorter and if the fronds are clustered a rosette is formed (Fig. 2, D). In long-creeping rhizomes, the much reduced trophophylls are scattered and often cling to the substrate. The modification of the trophophylls provides maximum photosynthetic surface for the area of the blades and orients them so that they have a moister, more protected environment. Under some circumstances, greater assimilation of carbon dioxide may be possible due to diffusion from the substrate of the respiratory products of bacteria, fungi, animals, and roots.

We need to know more about optimal times of appearance of sporophylls and trophophylls. Time of spore production, for example, may be highly adaptive, but we will not know this until we understand more about life cycles in the natural environment. In the Great Lakes area of North America, Hill and W. Wagner (1974) determined that thin-walled green spores are discharged in the spring and very thick-walled, non-green spores are discharged in the fall for the most part. This may have to do with germination and establishment, as the former group of spores are adapted for quick germination on mineral medium and the latter for slow germination on organic medium. The best season for release of thin-walled spores may be the spring when the greatest moisture and rainfall are available. Comparable conditions prevail in the tropics with respect to wet and dry seasons.

Drought conditions in tropical dry seasons may call forth extreme adaptations of the trophophylls, exaggerating those described above, as found in *Anemia* Sect. *Trochopteris* (*A. elegans* (Gardn.) Presl, *A. eximia* Taubert) with extremely small, flat laminae (cf. Mickel, 1962). The polypod, *Microgramma heterophylla* (L.) Wherry illustrates an elaborate form of heterophylly in a vining fern. This tropical American fern grows over dry limestone rocks and produces short, clasping, ovate leaves with blunt tips, in contrast to a more upright, elongate form of sterile leaf, and the long, erect, narrowly lanceolate fertile leaves. The completely flat, rosette-like sterile segment of the winter grapefern, *Botrychium lunarioides*, is probably adapted to growth only during winter months and is a device to capture maximum heat and light as well as to protect the tissues from sudden drying or cold shocks.

Whether or not sporophyll-trophophyll divergence has adaptive value with respect to parasites is presently purely speculative, but such a possibility should not be ignored. Collectors notice frequently, especially in the tropics, that soral structures seem to be especially liable to molds and to tiny insects that feed upon the spores and sporangia. Conceivably there are adaptive advantages to isolating the parts most likely to be eaten from those which photosynthesize. There is also a chance that the eating of sori and fertile pinnae by small animals may play some role in dispersal, especially of those spores that germinate beneath the soil or under leaf litter.

Although the onocleoid ferns are commonly cited by morphologists to illustrate foliar dimorphy, they are, in fact, unusual and not typical in several respects. Lloyd (1971) in his recent monograph of the systematics of the onocleoid ferns compared the fertile and sterile fronds of the three genera involved, but he did not compare them with other fern genera. Too little is known as yet about the rare Mexican genus *Onocleopsis* in its natural setting to evaluate it, but the two other genera, *Onoclea* and *Matteuccia*, show a number of unique features: The fertile leaves are (1) shorter than the sterile or equal to them, (2) their tissues are more dense and sclerified, (3) the sori, which are indusiate, are tightly encapsulated at maturity, and (4) the sporophylls persist much longer than the sterile fronds, which are early-deciduous in the autumn. What governs the final opening up of the bead-like pinnules is unknown, but in the eastern United States and Canada, where there is a strong winter-summer seasonality, the fertile units remain rigidly closed during the non-growing season and spore discharge is prevented. The hard, upright fertile leaves persist through the winter, covered with, or protruding through, the snow. The spores within stay green during their winter dormancy, and when they are released early in the spring they are ready to germinate immediately, thus taking advantage of the vernal moistness (Hill and W. Wagner, 1974). Although the sporophylls of *Onoclea* may sometimes equal or even surpass the trophophylls in height, those of *Matteuccia* are relatively much shorter, one-third or less the length of the trophophylls. In August and September, the sporophylls of *Matteuccia* are hard to see, buried as they are among the tall trophophylls and the other foliage of their swamp habitats. But in mid-winter all or most of the herbaceous plants have wilted and collapsed, so that the sporophylls are entirely exposed and easily swept by the wind. However, the actual discharge does not occur until March and April. Obviously the morphological peculiarities of these plants are correlated with the unusual seasonality of their spore production and release.

DISCUSSION

The noted Cornell University morphologist of the first half of this century, Arthur J. Eames, entertained some unusual theories about foliar dimorphism. In general he read the sequence just the opposite of the traditional interpretation and the one adopted here. In Eames' words (1938), "The segregation of vegetative and reproductive functions in different parts of the leaf, or in separate leaves, represents undoubtedly a primitive condition ... ; from this ancient dimorphism there has developed the condition —— often called monomorphism —— found in the majority of ferns, a blade serving for both vegetative and reproductive functions ... And from this there has developed a *new dimorphic condition* —— fertile and sterile leaves separate; this change has taken place independently in various genera ... " He thus postulated "ancient" dimorphism, which is the primitive state, leading to monomorphism, and then, once again to "modern" dimorphism. (Cf. his figure 175).

Eames cited three families —— Ophioglossaceae, Osmundaceae, and Schizaeaceae —— as representing the primitive type. All of these are of the type referred to in this paper as having "botryoidal" sporangial arrangement. Those of "Polypodiaceae" (i.e., all higher leptosporangiate ferns) represent Eames' "modern" type. We are not clear, however, upon what evidence he based his conclusions. The Ophioglossaceae are so isolated and so lacking in fossil evidence that we can only reason about what its course of evolution has been. We assume that it was derived from monomorphic fern-like plants because of analogies with repeated evolutionary sequences that we know in other groups. With respect to Osmundaceae, Miller (1971) concludes that "isomorphism represents the primitive state, incomplete dimorphism (only certain pinnae of a fertile frond modified for sporangia formation) is intermediate, and complete dimorphism is advanced," and he calls attention to the fact that fragments of laminate fronds bearing osmundaceous sporangia occur mainly in Jurassic sediments but range throughout the Mesozoic. Miller notes that "such fronds are generally included in the form genus *Todites*." Even though dimorphic pinnae in Osmundaceae were also found as early as the Jurassic and Triassic, this does not mean that this condition was primitive, any more than in families known primarily only today in which both monomorphic and dimorphic pinnae occur.

Also, as regards Schizaeaceae, the investigations of Mickel (1962, 1967) tend to contradict the conclusions of Eames. Mickel states that "although the change to dimorphism seems spectacular, in *Anemia* it is apparently a relatively simple and taxonomically minor one, which has occurred at least twice in the genus." He explains the unique leaf structure of typical anemias with their upright fertile basal pinnae to be derived from the typical fern leaf with unmodified basal pinnae (as in the closely related genus *Mohria*), and he describes a series of species, beginning with *Anemia colimensis* Mickel, with nearly monomorphic pinnae, and continuing through more and more differentiated forms, that finally terminates in such end-points as *A. rutifolia* and *A. millefolia*.

In view of the patterns seen in Osmundaceae and Anemioideae, and the total pattern of ferns in general, it is unlikely that there are two kinds of dimorphism, "primitive" and "modern," and that the latter arose from the former via a monomorphic stage. Such an hypothesis appears overly complex in the face of the over-all evidence. The hypothesis of one-way directionality is more economical and more probable. And when one considers the numerous analogous trends as are observed in other vascular plant orders such as Lycopodiales, Selaginellales, Equisetales and Cycadales, for example, the idea of reversal from dimorphic to monomorphic seems even less likely.

In his rather lengthy discussion of foliar dimorphy, Dickason (1946) wrote that "Evidently dimorphism has not arisen in response to any given set of environmental factors, and cannot be considered as adaptive." He based his conclusion, apparently, on the fact that dimorphy appears in plants of such widely different habits and habitats. Dickason was also concerned with the fact that "dimorphic and monomorphic species grow side by side." These conclusions are in keeping with a general negativism on Dickason's part with respect to adaptive values of most phylogenetic trends in ferns. He did concede, however, that dimorphy is an evolutionary advancement over monomorphy.

Whether Dickason's conclusion that there is no adaptive value in dimorphy is justified is questionable. Merely that foliar dimorphy occurs in a wide spectrum of habits and habitats does not necessarily militate against its being adaptive with respect to one or more of the factors outlined above. Furthermore, examples of non-adaptive and adaptive character-states in taxa that grow side-by-side are numerous in all plant communities. The point is that all plant species probably have mixtures of both adaptive and non-adaptive or neutral attributes.

Taxonomically there is no question that dimorphism is an extremely helpful character for making identifications. In *Genera filicum*, Copeland (1947) uses fertile-sterile dimorphism as a key character for over fifty genera. Nevertheless, it is not necessarily a valid character for establishing affinities or delimiting genera. For one thing, dimorphy is not a single character but an ensemble of different characters (Table 1), and any given expression invokes its own combination. Each manifestation must be analyzed accordingly. Furthermore, dimorphy has arisen in practically all families of ferns and in some of them probably several times. Table 2 summarizes the incidence in the various families and subfamilies of ferns. What is designated as "weak" involves only a few representatives of the taxon or only slight subdimorphism or both. "Strong" involves a majority of members and usually very distinctive sporophylls and trophophylls or well marked hemidimorphism. At the family level, dimorphy seems to be most pervasive in Ophioglossaceae, Plagiogyriaceae, Cheiropleuriaceae, Marsileaceae, and Salviniaceae.

In spite of the fact that dimorphy has been used to distinguish a number of fern genera, it is questionable whether it is of fundamental importance. Sometimes the dimorphic taxon is connected by intermediates to monomorphic taxa. Tagawa and Iwatsuki (Iwatsuki, 1961) erected the genus *Dimorphopteris* on the basis of its perfectly dimorphic fronds, the fertile pinnae so contracted as to be linearimoniliform. However, the type species, *D. moniliformis* from the island of Halmahera in the Moluccas has been shown by Holttum (1972) to be an extreme in a series of subdimorphic members of a section of the genus *Pronephrium*. Copeland, among others, paid considerable attention to sporophyll-trophophyll distinction in his classification, but this was apparently partially a result of his emphasis on convenience. In Table 3 are listed 12 genera (right-hand column) recognized by Copeland which may indeed be too little differentiated to justify separation from their parent genera.[4]

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[4] It may have some relevance that two recent students of the genus *Equisetum*, namely R. L. Hauke and C. N. Page, have rejected shoot dimorphism as a determining character for establishing sections and subgenera (Hauke, 1974).

The major taxonomic value of foliar dimorphy in ferns as a whole is at the species level. There are numerous examples of pairs of closely related species in which one member is essentially monomorphic and the other dimorphic. Such pairs deserve close examination; because of their genetic similarity their study may give us valuable insights into the evolutionary and adaptive significance of this phenomenon.

Table 1. Parallel and convergent changes associated with sporophyll-trophophyll differentiation. The primitive state for each character is undifferentiated or nearly so.

LEAF SIZE	Strongly unequal
ORIENTATION	Sporophyll erect, trophophyll spreading
PETIOLE LENGTH	Unequal
BLADE OUTLINE	Sporophyll narrow, trophophyll wide
BLADE CUTTING	Sporophyll usually more divided; trophophyll usually less divided (but exceptions)
LAMINAR WEBBING	Sporophyll with reduction or loss of lamina; trophophyll unchanged or with increase
LAMINAR MARGINS	Sporophyll commonly smoother; trophophyll more toothed
VENATION COMPLEXITY	Sporophyll most commonly simplified by vein loss; trophophyll more complex
VEIN INTERVAL	Sporophyll veins more remote; trophophyll veins more approximate
MESOPHYLL	Sporophyll non-green, soft; trophophyll green, more compact and rigid
EPIDERMIS	Sporophyll with fewer stomates and larger, smoother-walled cells; trophophyll with normal epidermis
SORIATION	Sori concentrated, often confluent into acrostichoid condition or grouped into botryoidal condition
ENCAPSULATION	Sporangia, at least while young, covered by rolled lamina
SEASONALITY	Sporophyll separated from trophophyll in time of appearance, usually earlier but may be later
DURATION	Sporophyll short-lived; trophophyll long-lived. Rarely otherwise

Table 2. Parallel and convergent evolution of foliar dimorphy in ferns. Relative incidence and main types in different families or subfamilies. Letters refer to dimorphic types in Figure 1.

ABSENT TO WEAK	MODERATE	STRONG TO COMPLETE
Marattiaceae (D)	Polypodioideae (B, D)	Ophioglossaceae (C)[1]
Gleicheniaceae	Lygodioideae (B)	Osmundaceae (B, D, E)
Matoniaceae	Dryopteridoideae (B, D, F)	Plagiogyriaceae (D)
Dipteridaceae	Blechnoideae (D)	Anemioideae (C)[2]
Loxogrammeoideae		Ceratopteridoideae (D)
Grammitoideae (B, D)		Marsileaceae (C)[4]
Schizaeoideae (D)[3]		Salviniaceae (D)[5]
Adiantoideae (D)		
Vittarioideae		
Cyatheoideae		
Hymenophylloideae		
Lindsaeoideae		
Asplenioideae		
Azollaceae		

[1] Fertile spike composed of fused basal fertile pinnae.
[2] Fertile basal pinnae not fused, except in some cases to the petiole.
[3] Fertile blade drastically reduced and petiole exaggerated. Sterile petioles maintained at maturity in *Schizaea pusilla* Pursh.
[4] Type "C" if sporocarps are modified fertile pinnae.
[5] Sporophyll is the immersed root-like leaf.

Table 3. Genera of close affinity which were discriminated by Copeland (1947) on the basis of fertile-sterile leaf dimorphism.

MONOMORPHIC OR SUBDIMORPHIC PARENTAL GENUS		DIMORPHIC SEGREGATE
	POLYPODIACEAE	
Pleopeltis		Lemmaphyllum
Pleopeltis		Marginariopsis
Colysis		Dendroglossa
Aglaomorpha		Merinthosorus
Crypsinus		Pycnoloma
	ADIANTACEAE s. l.	
Pteris		Neurocallis
	CYATHEACEAE s. l.	
Trichomanes		Feea
	ASPLENIACEAE s. l.	
Phanerophlebia		Cyclodium
Ctenitis		Psomiocarpa
Tectaria		Tectaridium
Tectaria		Hemigramma
Tectaria		Quercifilix

LITERATURE CITED

Bower, F. O. 1923. The Ferns. Vol. I. Analytical Examination of the Criteria of Comparison. Cambridge U. Press.

Bower, F. O. 1928. The Ferns. Vol. III. The Leptosporangiate Ferns. Cambridge U. Press.

Copeland, Edwin B. 1907. The comparative ecology of San Ramon Polypodiaceae. Philippine Jour. Sci. **2** (no. 1): 1–76, pl. 1–4.

Copeland, Edwin B. 1947. Genera filicum. Chronica Botanica, Waltham, Mass.

Dickason, Frederick Garrett. 1946. A phylogenetic study of the ferns of Burma. Ohio Jour. Sci. 156 (no. 2): 73–108.

Eames, Arthur J. 1936. Morphology of Vascular Plants. Lower Groups. McGraw-Hill Co., New York.

Gupta, K. M. and T. N. Bhardwaja. 1956. Indian Marsileas: their morphology and systematics. Jour. Bombay Nat. Hist. Soc. **53**: 423–444, pl. 1–3.

Gupta, K. M. 1962. Marsilea. Botanical Monograph No. 2 Council of Sci. and Ind. Res., New Delhi.

Hauke, Richard L. 1974. The taxonomy of Equisetum —— an overview. New Botanist **1**: 89–95.

Hill, Royce C. and W. H. Wagner, Jr. 1974. Seasonality and spore type of the pteridophytes of Michigan. Mich Bot. **13**: 40–44.

Holttum, R. E. 1938. The ecology of tropical pteridophytes. *In* Verdoorn, F., Manual of Pteridology, pp. 420–450. Martinus Nijhoff, The Hague.

Holttum, R. E. 1939. The genus Lomariopsis in Madagascar and the Mascarene Islands. Notul. Syst. **8**: 48–62.

Holttum, R. E. 1972. Studies in the family Thelypteridaceae. The genus Pronephrium Presl. Blumea **20**: 105–126.

Iwatsuki, Kunio. 1961. Taxonomic studies of Pteridophyta VI. Acta Phytotax. Geobot. **19**: 1–11.

Labouriau, Luiz Gouvêa. 1958. Studies on the initiation of sporangia in ferns. Arquivos do Mus. Nacional, Rio de Janeiro **46**: 119–202.

Lommasson, Robert C. and C. H. Young, Jr. 1971. Vascularization of fern leaves. Amer. Fern Jour. **61**: 87–93.

Lloyd, Robert M. 1971. Systematics of the Onocleoid ferns. Univ. Calif. Publ. Bot. **61**: 1–93.

Mickel, John T. 1962. A monographic study of the fern genus Anemia, Subgenus Coptophyllum. Iowa State Jour. Sci. **36**: 349–482.

Mickel, John T. 1967. The phylogenetic position of Anemia colimensis. Amer. Jour. Bot. **54**: 432–437.

Nozu, Yoshitomo, 1968. Studies on the leaves of the Ferns. I. The dissimilarities of the fertile and sterile fronds in some ferns. Jour. Fac. Sci., Univ. Tokyo Sec. III. **10**: 13–27, pl. 2.

Wagner, W. H. Jr. 1965. Paraphyses: Comments on recent papers. Taxon **14**: 299–302.

Wagner, W. H., Jr. 1973. Some future challenges of fern systematics and phylogeny. *In* Jermy, A. C., Crabbe, J. A., and Thomas, B. A. (ed.), "The Phylogeny and Classification of the Ferns." Bot. Jour. Linnaean Soc. **67** (Suppl. No. 1): 245–256.

Wagner, W. H., Jr., D. R. Farrar, and B. W. McAlpin. 1970. Pteridology of the Highlands Biological Station Area, Southern Appalachians. Jour. Elisha Mitchell Sci. Soc. **86**: 1–27.

White, Richard A. 1971. Experimental and developmental studies of the fern sporophyte. Bot. Rev. **37**: 509–540.

Wieffering, J. H. 1964. A preliminary revision of the Indo-Pacific species of Ophioglossum (Ophioglossaceae). Blumea **12**: 321–337.

A Note on Dendrobium serpens (Hk.f.) Hk.f.

by

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In his "Orchids of Malaya", Holttum (1964 : 319) lists *Dendrobium serpens,* adding to his description that "more information is wanted about this species". We listed it in "Orchids of Thailand" (Seidenfaden & Smitinand 1960 : 244) based on Holttum's information that *Dendrobium virescens* Ridl. should be considered a synonym, and remarked that the plant was found once in Tomoh in Peninsular Thailand just north of the Malayan border but we had never ourselves seen the plant.

In the summer of 1970 Smitinand and I went on an orchid hunting expedition to the southernmost provinces of Thailand. Among the plants collected near the border of Malaya at Waeng Forest Station west of Sungai Kolok was a trivial *Dendrobium,* which was brought to the hothouses in Copenhagen in the hope that it would produce the flowers necessary for the identification. No flowers appeared for years, but when in the spring of 1975 we experimentally raised the average humidity in the houses, several of the plants showed increased activity, and, in May 1975 it produced flowers, making it possible to identify it as *Dendrobium serpens* by means of Holttum's keys. This led to the small study related below, giving some bits of the information wanted by Holttum.

During the period of printing of the orchid part of "The Flora of British India" Hooker f. continued to receive new material, both in the form of new collections in the field and as drawings, mainly from the Calcutta herbarium. This necessitated the addition of a supplement to his treatment, found in the sixth volume of "Flora of British India" containing a lot of important, although too often overlooked, information.

Among the drawings received from Calcutta was one of a *Dendrobium* of the *Pedilonum* section, said to represent a plant growing at "Rangoon", brought by Mr. Gilbert, a resident of Moulmein, where he succeeded Parish, and on a more modest scale tried to take up the work of this great botanist, sending to Europe herbarium specimens of orchids, often accompanied by sketches of which several are found in Reichenbach's herbarium in Vienna. In the present case Gilbert must have sent a living plant, because when Hooker f. received the drawing from Calcutta, to it was attached a single dried flower, said to have developed in the Garden at Calcutta in November 1884. As to my knowledge the species has never turned up in the Pegu area, I feel we must not exclude the possibility that the plant was not at all found "at Rangoon" but rather, brought up to Rangoon from Moulmein for shipment to Calcutta. Hooker f. called the plant *D. panduriferum.*

Another drawing received from Calcutta, made after a plant collected by Kunstler in Perak and flowering in Calcutta in May 1884, prompted Hooker f. to describe it as a variety of Gilbert's plant, calling it *Dendrobium panduriferum* var. *serpens.* Of this he evidently got no plant material and had in his description to rely solely on the drawing. This too he later reproduced (1895: 10, Pl.16), at which time he reached the opinion that the two entities were different enough to justify considering the Perak plant a separate species, *Dendrobium serpens.*

Very little information on these two taxa has appeared since. Grant (1895: 108) copied Hooker f. in his Burma list, while Ridley in his paper on the orchids of

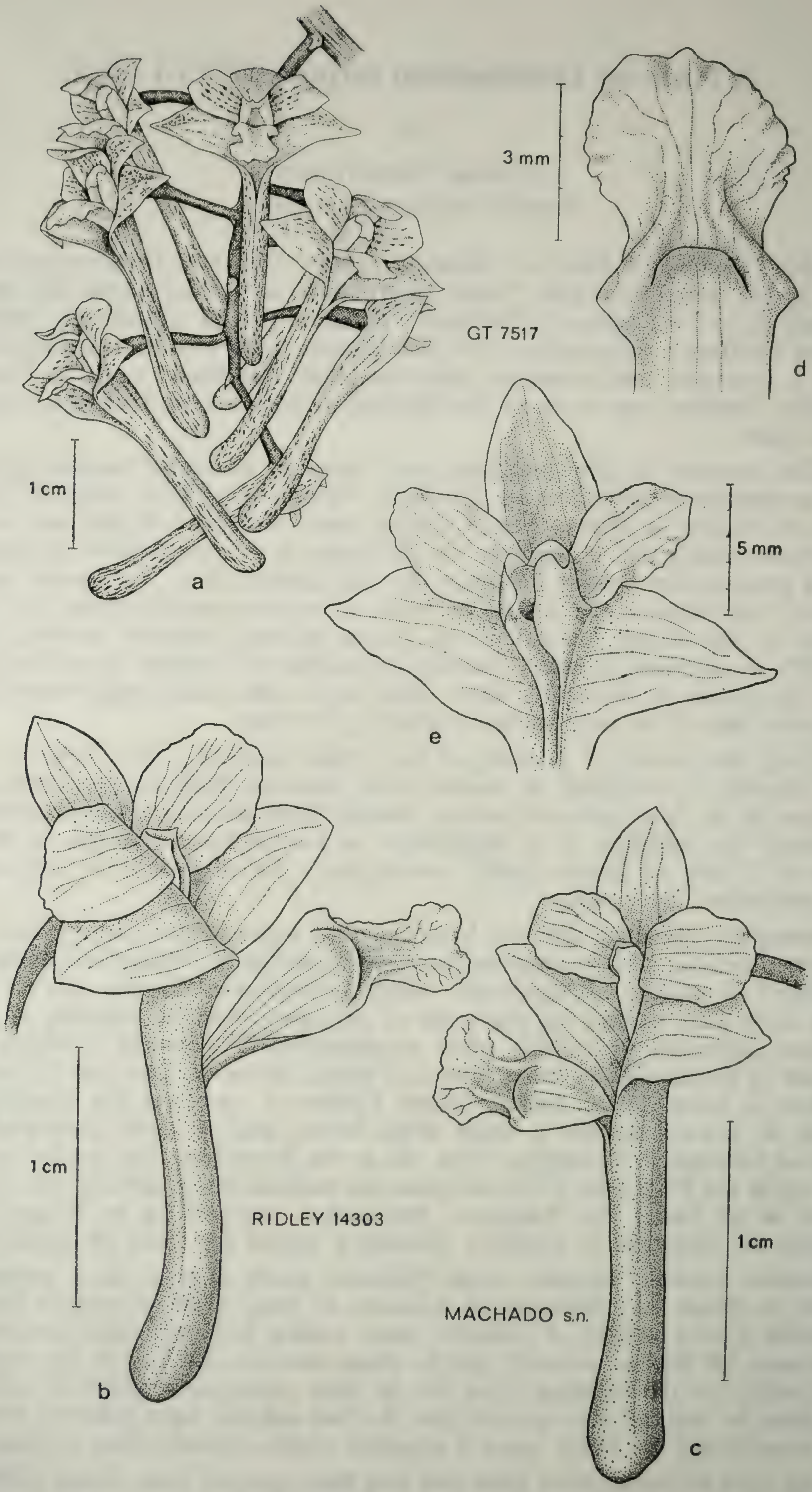

Fig. 1. *Dendrobium serpens* (Hk. f.) Hk. f. a. inflorescence from a fresh Thai specimen, b. flower from the Temengo specimen, c. flower from the type specimen of *D. virescens*, d. epichile and e. flower without lip and mentum from the Thai specimen.

the Malay Peninsula (1896) overlooked Kunstler's Perak plant which he subsequently listed in his "Materials" (1907:47), and, in his "Flora of the Malay Peninsula" (1924:47) we learn that he had identified one of his own collections as being Kunstler's plant, giving the locality as Ulu Temengo (= Temengor) on an island in the Kertai River.

Already in 1896 Ridley had, however, introduced a new taxon, *Dendrobium virescens,* based on a collection made by Machado further to the Northwest, at Tomo (spelled by Ridley as Tomoh) which I believe is on the Thai side of the border and, in the "Materials" we learn that he had identified a plant collected at Taiping in Perak by Curtis, — the latter is repeated in the 1924-paper.

In his large monograph on Dendrobium, Kränzlin (1910) lists *Dendrobium virescens* and *D. panduriferum* without adding any new information, he places them in two different subsections of the *Pedilonum*-section, although they might be considered conspecific, cfr. below. *Dendrobium serpens* he choses to consider a synonym of Reichenbach's *Dendrobium ionopus,* a plant said by Reichenbach to have come from Burma. Hooker f. had originally suggested that his var. *serpens* could be the same as *D. ionopus,* but later (1895:11) he indicated that he was convinced of the contrary; Kränzlin seems to disregard this viewpoint, while both Ridley and Holttum ignore Kränzlin's opinion.

In response to "more information" sought by Holttum, I got with the kind assistance of Dr. Chang the available material from Singapore, at the same time receiving from Vienna the material kept in the Reichenbach herbarium under the name of *Dendrobium ionopus.*

There seems no doubt that the recently found Thai plant is identical with both the Tomo plant which is the type specimen of *Dendrobium virescens* Ridl. and with the plants from Ulu Temengo and Taiping. The most characteristic features are details of the lip, see Fig. 1. There is a half-moon shaped transverse callus at the base of the epichile at the side of which the edges fold into ears continuing as longitudinal somewhat converging folds on the blade of the epichile. There is no fattening on the epichile, the whole of it is of very thin texture, which is not very clear on the drawings Hooker f. received from Calcutta; based only on these, Hooker described the blade as "cordate above and below, slightly constricted at the middle".

When comparing the original drawing which was the only basis for Hooker's analysis, with the plate published by Hooker of *Dendrobium panduriferum* it is important to recall that here the details of the flower are based on Hooker's own dissection of a flower he received with the habit drawing. It is tempting to suggest that after moistening or cooking the flower, any folds and ears in the thin material would vanish, and a lip like the one found in the material we have from Thailand and Malaya of *D. serpens* would look pretty much like Hooker's drawing of the lip of *Dendrobium panduriferum,* described by Hooker as "deeply constricted with auricle-like sidelobes", the transversal callus is the same. I am therefore quite convinced that *D. panduriferum* and *D. serpens* are the same species. The only depiction of a flower in front view in the habit drawing of *D. panduriferum* (drawn in India after fresh material) shows, in my opinion, an epichile indistinguishable from the one shown in the Indian picture of *D. serpens,* and the other differences mentioned by Hooker seem not very convincing. I feel, however, that it would be too hasty to reduce *D. serpens* to a synonym, perhaps it is safer to wait until fresh material has been obtained of plants from "Rangoon"; repeating Holttum's words that "more information is wanted", my preliminary summary on *D. serpens* therefore reads as follows:

Dendrobium serpens (Hk. f.) Hk. f., Ann. Bot. Gard. Calc. 5: 10, T. 16, 1895.— Ridley 1907:51; idem 1924:47; Holttum 1964: 319; Seidenfaden & Smitinand 1960:244.

Dendrobium panduriferum var. *serpens* Hk. f., Fl. Brit. Ind. 6:186, 1890.

Dendrobium virescens Ridl., Journ. Linn. Soc. 32:259, 1896.—F. N. Williams 1904: 368; Ridley 1907:51; Kränzlin 1910:100; Ridley 1924:47.

Dendrobium ionopus auct. non Rchb. f.: Kränzlin 1910: 122 (p.p.)

Distribution: Thailand: Legeh at Tomoh (Macado s.n. SING!, type of *Dendrobium virescens*); Near Waeng Forest Station, Narathiwat 250m (GT 7517 C!).

Malaya: Perak (drawing in Calcutta after a plant sent by Kunstler, type); Ulu Temengo on an island in Kertai River (Ridley 13303 SING!); Taiping (Curtis s.n. SING)!); presumably also Karangan, Kedah (Haniff s.n. SING!, insufficient material).

Now, on *Dendrobium ionopus* Rchb. f. of which Kränzlin considered *Dendrobium serpens* a synonym:

The material of this taxon in Herb. Reichenbach consists of two sheets. The one carrying the handwritten original description (No. 41205) contains a single dissected flower which, under the number 3769, had been sent by Low in November 1882 and said to originate in Burma, further, some rough coloured sketches by Reichenbach of that flower, and a copy of one of Day's drawings. I later saw the original of that drawing in Day's rich manuscript collection in Kew, made in November 1882, and a note gives the same information that it was imported by Mr. Low from Burma. The other sheet (No. 41204) contains an inflorescence also sent by Low, with whom it flowered in 1881; it is noted that the collector was Boxall and that it originated in the Philippines.

The flowers on the two sheets are identical. The most important characteristics are the two low triangular lateral calli near the edge at the base of the epichile (these are both in Reichenbach's and Day's drawings coloured dark red-purple), and the obtuse tooth in the "spur", see Fig. 2. The flower is quite different from that of *D. serpens*, and Kränzlin was wrong.

But seeing my sketches of *D. ionopus*, Dr. Garay called my attention to the figure of a taxon described in 1908 by Kränzlin as a new species, *Dendrobium epidendropsis*, based on one of Loher's plants. This is clearly the same as Low's plants. *D. epidendropsis* has later been recorded several times from Luzon.

Here again, it is at hand to be suspicious about the old information. Considering the general tendency during the later part of the last Century to be less exact (and often with purpose misleading) on the origin of commercially introduced plants, I feel convinced that the flower Low sent to Reichenbach and Day in 1882 as "from Burma" is from the same plant or the same consignment as the one sent a year before as being a Boxall-collection from the Philippines, and I feel we should exclude the record from Burma.

Finally, I would suggest that the photograph reproduced under the name *Dendrobium O'Brienianum* by Davis & Steiner (1952: 120) looks more like *Dendrobium ionopus;* Kränzlin's drawing of *D. O'Brienianum* (1910: Fig. 5 N-O) has a much more slender mentum, also the photograph shows a pair of dark spots somewhere at the base of the lip, not mentioned in Kränzlin's colour description, but, naturally, the photo is not sharp enough for a sure identification.

My knowledge on *Dendrobium ionopus* could therefore be summarized as follows:

Dendrobium ionopus Rchb. f., Gard. Chron. 1882, 2: 808.—

Hooker f. 1890: 732, Grant 1895: 100; Kränzlin 1910: 122. (excl. syn. *D. serpens*).

Dendrobium epidendropsis Krzl., Orchis 2: 79, Fig. 12, 1908, syn. nov. — Ames 1909: 598; Kränzlin 1910: 106; Ames 1915: 123; idem 1925: 348.

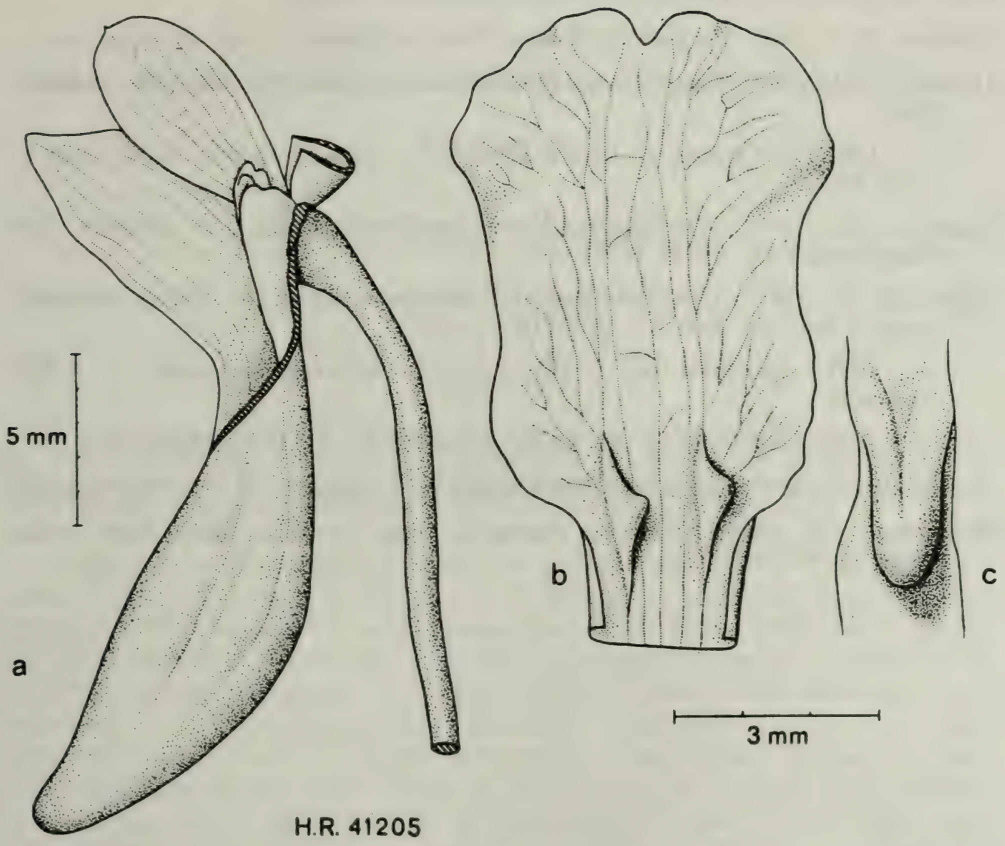

Fig. 2. *Dendrobium ionopus* Rchb. f. Type specimen. a. the only mutilated flower, with dorsal sepal, a petal and part of a lateral sepal missing, lip removed, b. epichile of lip, c. tooth in mentum.

Dendrobium O'Brienianum auct. non Kränzlin: Davis & Steiner 1952: 120?

Distribution: ? Burma: s.n. (Low 3769 Herb. Reichenbach 41205!, type, origin improbable).

Philippines: sine loc. (Boxall s.n. Herb. Reichenbach 41204!; Loher s.n., type of *D. epidendropsis;* Lyon 118 and 161, fide Ames); Lamao River, Bataan, Luzon (Borden 2109 and Elmer 6839, fide Ames); Rizal, Luzon (Ramos 3060, fide Ames).

Literature Cited

Ames, O., 1909: Notes on Philippine orchids with descriptions of new species 1. Phil. Journ. Sci. 4, 5: 593–600.

——— . 1915: Orchidaceae 5. The Genera and Species of Philippine Orchids. Boston, 271 pp.

——— . 1925: Enumeration of Philippine Apostasiaceae and Orchidaceae. Bur. Sci. Publ. No. 18: 252–463. Manila.

Davis, R. S. & M. L. Steiner, 1952: Philippine Orchids. New York, 270 pp.

Grant, B., 1895: The Orchids of Burma. Rangoon, 416 pp.

Holttum, R. E. 1964: Orchids of Malaya. Flora of Malaya 1. 3rd. ed. Singapore.

Hooker, J. D., 1890: The Flora of British India 5: 667–864, 6: 1–198. Ashford, Kent.

——— . 1895: A Century of Indian Orchids. — Ann. Roy Bot. Gard. Calc. 5: 1–68, Pls.

Kränzlin, F., 1910: Orchidaceae-Monandrae-Dendrobiinae, in Engler: Das Pflanzenreich IV. 50. II. B. 21.

Ridley, H. N., 1896: The Orchideae and Apostasiaceae of the Malay Peninsula. Journ. Linn. Soc. Bot. 32: 213–416.

——— . 1907: Materials for a Flora of the Malayan Peninsula 1: 7–233. Singapore.

——— . 1924: The Flora of the Malay Peninsula 4: 4–233. Ashford Kent.

Seidenfaden, G. & T. Smitinand: The Orchids of Thailand 2, 2: 185–326 Bangkok.

Williams, F. N., 1904: Liste des Plantes connues du Siam. Bull. Herb. Boiss. 2. ser. 4: 362–372.

Notes on the Systematy of Malayan Phanerogams XXV.*

Araliaceae

by

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Abstract

Two genera are reduced to synonymy, *Wardenia* King to *Brassaiopsis* Decne. & Planch., and *Acanthophora* Merr. to *Aralia* L. Critical notes on some other genera, some new combinations, and two new species, *Brassaiopsis minor* and *Schefflera singularis*, are published. A brief growth analysis of *Arthrophyllum diversifolium* sensu King is presented.

In the course of preparing the treatment of Araliaceae for Vol. 3 of the "Tree Flora of Malaya" a number of problems involving not only the recognition and delimitation of species, but also of genera, have arisen. Two undescribed species have been encountered and are published here. Equally important, the status of two hitherto monotypic genera, *Wardenia* King and *Acanthophora* Merr., has been reassessed, and it has been concluded that they should be reduced to synonymy under *Brassaiopsis* Decne. & Planch. and *Aralia* L. respectively. The largest genus of the family in Malaya, *Schefflera* J. R. & G. Forst., is currently being revised by D. G. Frodin of the University of Papua New Guinea. In his dissertation (Cambridge University 1971) he has taken a broad view of *Schefflera*, incorporating within it three genera recognized by Ridley in his Flora of the Malay Peninsula (vol. 1, 1922), *Brassaia* Endl., *Scheffleropsis* Ridl., and *Tupidanthus* Hk. f. & Thoms. In a recent publication (1970) Philipson has reviewed the genus *Gastonia* and remarked on a species which occurs in Malaya, which was not in Ridley's Flora. The genus *Acanthopanax* Miq. has been found to occur in Malaya, the sole Malayan species being *A. malayana* Henderson (Gdns Bull. Sing. 7: 105–6, pl. 23. 1933). Ridley himself described a second species of *Hederopsis* King some years after his Flora was published (*H. major* Ridl. in Kew Bull. 124. 1929). The genus *Polyscias* Forst. is not in Ridley's Flora, but is represented in the Peninsula by several species found in cultivation.

Thus at present there are known to occur in Malaya ten genera of Araliaceae: *Acanthopanax, Aralia, Arthrophyllum, Brassaiopsis, Dendropanax, Gastonia, Hederopsis, Polyscias, Schefflera,* and *Trevesia*. If *Tupidanthus* is maintained as a distinct genus, as advocated by Philipson (pers. comm.), the total is eleven.

The genus *Aralidium* Miq. was assigned to Cornaceae in Ridley's Flora, but placed in Araliaceae by Corner (Wayside Trees of Malaya 1: 154. 1940 & 1952). After considerable preliminary study it is deemed preferable to exclude it from Araliaceae on account of its lack of resin canals, among other characters. Whether it should rejoin Cornaceae or find some other position is a problem still under study.

Aralia L.

Ridley reported three species of *Aralia* from the Malay Peninsula, *A. thomsonii* Seem., *A. armata* (Wall. ex G. Don) Seem., and *A. ferox* Miq. Merrill (Philipp. J. Sci. 13, Cr, 316–318, 1918) showed that Philippine and Celebes specimens determined as *A. ferox* Miq. were not that species at all, and because of the climbing habit created a new genus *Acanthophora* for these plants with *A. scandens* Merr. as the sole species. Later, van Steenis (Bull. J. Bot. Buitenz. ser. 3, 17 : 390, 1948) added further determinations and included the "A. ferox" of Ridley's flora, adding the genus *Acanthophora* to the known Malayan Araliaceae.

The species *Acanthophora scandens* Merr. is certainly distinct. It has recently again been collected along the Ginting Highlands Road, Pahang (*Stone 12016*). A study of this material and a review of the pertinent literature suggest however that the generic status for this species is highly dubious, its sole claim to it being the lianoid habit. Since most species of *Aralia* are shrubs or trees (or herbs) the liane habit does stand out. On the other hand there are many genera known which include species with this habit along-side others which are trees or shrubs, witness *Schefflera,* and outside the *Araliaceae, Derris* (Leguminosae), to name but two examples. In this view I am supported by D. G. Frodin (Misc. Rec. Fl. Mal. Found. III: 8. 1973).

In any case there is a nomenclatural reason why the name *Acanthophora* Merr. 1918 cannot be used, even if the generic concept it denotes were considered worth retaining. This is the generic name *Acanthophora* Lamouroux 1813, applied to a taxon of Rhodophyceae (Red Algae). This name was obviously overlooked by Merrill, when he created what was, in fact, a later homonym.

Aralia scandens (Merr.) T. D. Ha, Novost. Sist, Vysh. Rast. 11: 229. 1974.

Acanthophora scandens Merr. Philip. J. Sci. C, 13: 316–318. 1918.

Aralia ferox sensu Ridley (non Miquel) in Fl. Mal. Pen. 1: 873. 1922.

(Not *Acanthophora* Lamouroux, 1813 (Algae)).

Distrib. — Malaya, Philippines, Celebes. In Malaya: Perak, Pahang, and Selangor. Fig. 1.

Arthrophyllum Blume

Among the Araliaceae this is one of the more clearly distinct genera, rather easily recognized by its pinnate leaves and 1-celled ovary and fruit. The species are another matter. They are poorly described, mainly because of poor inadequate collections, and badly discriminated. Most are rather difficult to distinguish. Those in the Peninsula in particular are in a state of confusion because of the too-optimistic classification by Ridley. In the Flora (I: 885) Ridley lists 8 species. These cannot be reached through the key and cannot be recognized from the descriptions which are too brief and contain errors of fact. The available specimens, including types and syntypes, even when examined, are not always decisive. Of the 8 species listed by Ridley, four seem to me reasonably clear; the others are to be considered as synonyms or as varieties of these four.

The main point of this note is to describe in some detail the basic growth pattern of the largest of the Malayan *Arthrophyllums.* This plant was called *A. diversifolium* by Clarke, King and by Corner, while Ridley called it *A. ovalifolium.* Since it never possesses bipinnate leaves, it does not correspond very well with the former. Apparently it is not the same as the latter. The nomenclature will be treated in a separate paper by W. R. Philipson. At any rate, it is clear that throughout the lowlands of Malaya, there is a single, rather uniform tall *Arthrophyllum* species,

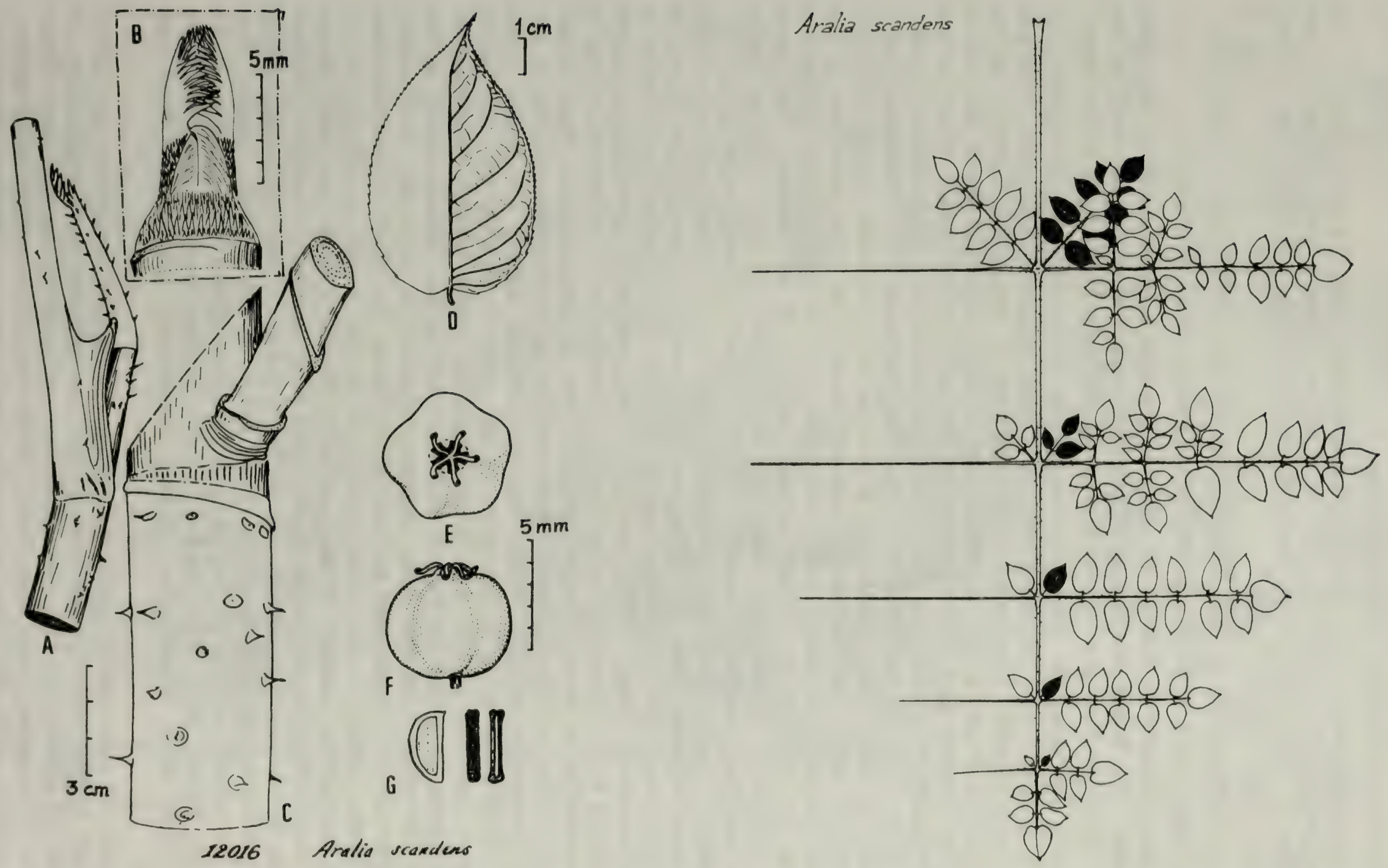

Fig. 1. *Aralia scandens* (Merr.) T.D. Ha. *Left:* details of shoot apex. A:—shoot apex with leafbase showing lobed stipule and young developing leaf. B:—still younger leaf, upper side, with overlapping stipular flanges (centre). C:—stem segment with branch-base. D:—leaflet. E:—top view of fruit. F:—side view of fruit. C:—seeds in side view, end view, and longisection. *Right:* diagram of leaf structure, "Stipellar" pinnae shown in black.

which often enters waste ground as a pioneer regrowth plant. Its trunk eventually branches sparsely, and the trees may reach a height of over 15 m. This is the plant referred to here in the following description.

Arthrophyllum sp. — A. diversifolium sensu King, Mat. Fl. Mal. Pen. in J. R. As. Soc. Bengal, 47, II (1): 59. 1898, non Blume; sensu Corner, Wayside Trees of Malaya 1: 155, 1952. — A. ovalifolium sensu Ridley, Fl. Mal. Pen. 1 : 885, 1922, non Jungh. & De Vriese. Fig. 2.

A. congestum Ridl. J. Fed. Mal. St. Mus. 10: 137. 1920; Flora 1: 887. 1922.

Lectotype: SELANGOR: Klang Gates, *Ridley 13421.* (SING).

Although Ridley's binomial *A. congestum* applies unquestionably to this plant there seems little doubt that it is to fall into synonymy when a wider study of the group is made, and this is to be reported on by Professor Philipson in this volume.

Ridley attributed the name *A. ovalifolium* to Miquel, but the authors, as stated by Miquel, were Junghuhn and De Vriese. Miquel's description does not seem to be a different interpretation. In describing *A. congestum* Ridley notes the flowers as with 4 petals, but examination of the type collection shows that this is wrong; the flowers, as would normally be the case, are 5-merous. There are no other characters to distinguish this from the common, arboreous lowland species which Ridley calls *A. ovalifolium.* In accepting this name for a Malayan species, the chance of error is not small, and it remains to be checked against authentic specimens. At any rate, the species intended here is the most abundant of the Malayan lowlands, at least on the west coast, and is usually, when mature, a branched tree up to 14 m tall with a trunk reaching 30 cm diameter. The leaves on the main erect (orthotropic) stems are closely spiralled; they are large, once-pinnate, reaching a length of 2 meters, with 12–14 pairs of large leaflets (Fig. 2–2). Like Ridley, I have never seen a bipinnate leaf in any Arthrophyllum; on this basis I have refrained from identifying our plants with *A. diversifolium* Bl. or its synonyms, though this is the name used by King in the 'Materials' and Corner in "Wayside trees of Malaya (1940)" and found on a number of herbarium specimens in SING and KEP. According to the available descriptions *A. diversifolium* has at least some bipinnate leaves. It is possible that hasty observation of our plants would suggest that they too bear bipinnate leaves, but this arises through confusion of the axillary determinate branches (which bear the flowering shoots) with leaves. These axillary branches (Fig. 2–3) are more or less plagiotropic (though not usually horizontal), and bear at their widely spaced swollen nodes opposite bipinnate but reduced leaves, or nearer the tip, whorled and even further reduced leaves; in the axils of the latter arise the short flowering shoots (Fig. 2–3 and 2–9), which themselves have 1–3 nodes with pairs of simple leaves (Fig. 2–6). The resemblance of the lateral branch to the rachis of one of the big leaves is striking, but its position and smaller number of nodes serve to identify it. Since the leaves borne on the lateral branches are much smaller, and with successively reduced numbers of nodes, they are easy to collect, and hence are found on most herbarium sheets; but they are not really representative of the plants, as besides being smaller, they are not or scarcely asymmetric, which is the usual condition of the leaflets on the lower, big leaves. Also, their number of lateral nerves may be smaller. These circumstances make identification of such fragmentary collections difficult and hesitant.

Plants of this species generally remain unbranched until they are about 2.5 m tall; at this stage they may branch, but the branches are recapitulations of the trunk, i.e. orthotropic with spiral phyllotaxy and more or less equivalent. These may grow to an equal length, then flower. Flowering is by inception of the axillary lateral branches with distichous or whorled phyllotaxy, as described above; but new orthotropic shoots arise from other axils providing relays. The lateral shoots are strongly determinate in growth and reach about the same length as the big

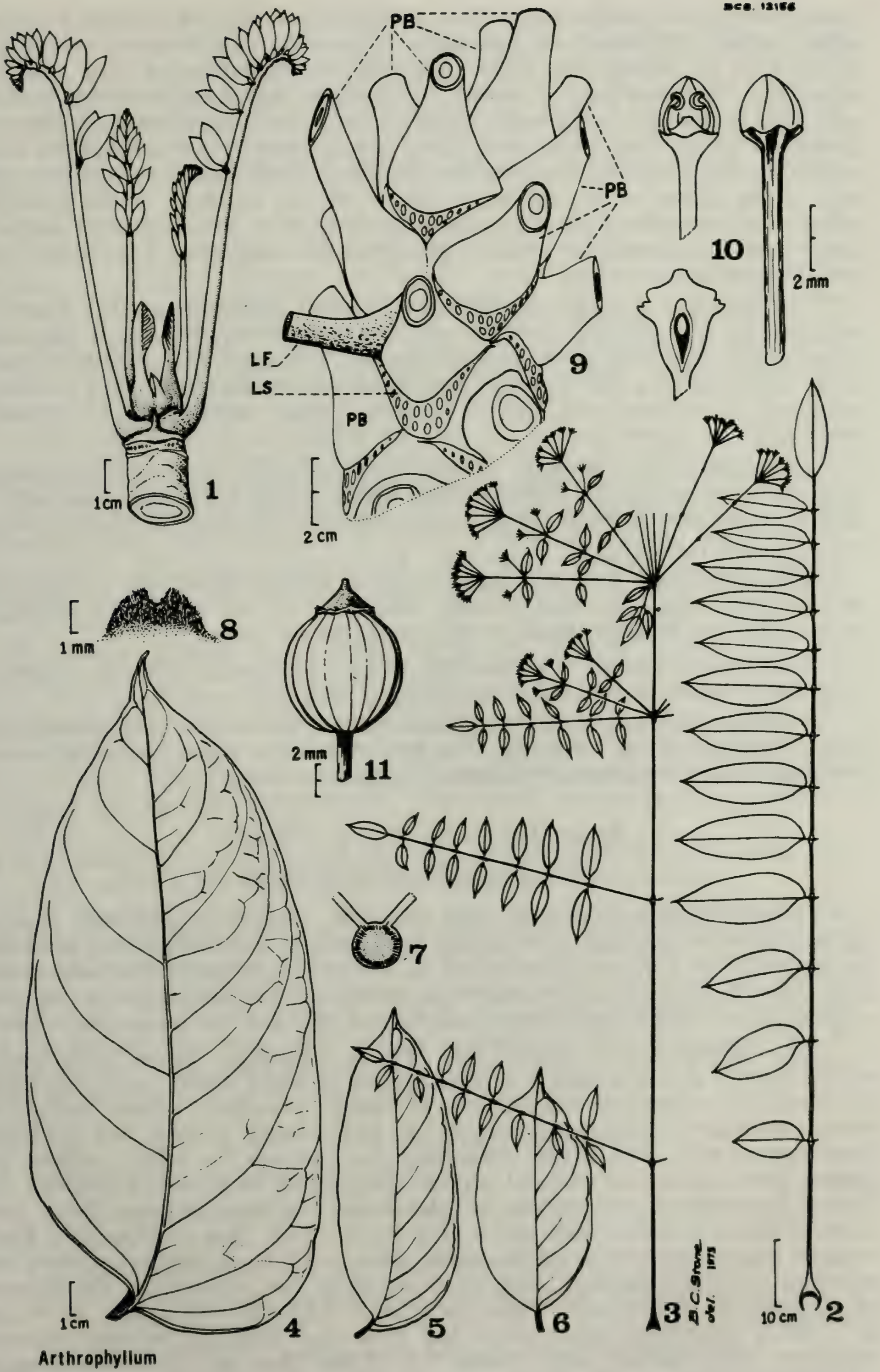

Fig. 2. *Arthrophyllum* sp. (*A. diversifolium*, sensu King). Aspects of its morphology. 1:—First-order shoot. 2:—Pinnate leaf of first-order shoot. 3:—Second-order shoot. 4:—Medial leaflet from leaf of first-order shoot. 5:—Medial leaflet from lowest leaf of second-order shoot. 6:—Simple leaf from third-order (flowering) shoot. 7:—Cross-section of leaf rachis. 8:—Axillary bud. 9:—Apex of first-order shoot bearing second-order shoot branches (PB) and their axillant leaves (LF) or their scars (LS). 10:—Floral details. *Stone 12156*.

pinnate leaves of vegetative stems. Their resemblance to rachises has been mentioned above; in fact, the immediate appearance suggests that the flowering umbels arise in the axils of leaflets, but close study dispels this impression. The big lower leaves always have at least 10 nodes, but the upper leaves on the lateral branches may have as few as 1 or 2 nodes (these leaves usually immediately subtend the flowering shoots). The reversion to spiral arrangement at the apex of the lateral branch is abrupt and striking. On the flowering shoots, there are umbels in the axils of the leaves on the median nodes as well as clustered at the apex. The inflorescence, therefore, consists, strictly speaking, of a pseudumbellate cluster of simple umbels, although superficially the appearance suggests a 2- or even 3-compound umbellate structure.

The leaflets of a single leaf often have unequal laminal areas. The whole row of leaflets on one side (e.g. the "left" or "right" side) may be slightly larger than those on the other side of the rachis. However, if there is this 'overdevelopment' of the right side of a leaf, then the next higher leaf of the spiral often has its left side similarly overdeveloped, and the successive higher leaves reveal an alternation continuing this pattern.

The nodes of the leaf rachis are closer nearer the leaf apex, and the internode distance is correlated approximately with leaflet width, being about the same or slightly more than the width of the nearest leaflets. The lower internodes elongate first and most rapidly.

The stipules are short and connate into a narrow ligular rim, ciliate in the very youngest stage but soon glabrate. Internodes on the orthotropic shoots are so short that the sheathing bases of the petioles are in contact.

The fruits are about 5–6 mm long, globose to broadly ellipsoid, capped by the remnant calyx rim and the short persistent conic style.

Seedlings. Seedlings of this species are epigeal, with a pair of opposite bluntly ovate cotyledons about 1 cm long. The first several true leaves are simple, ovate-acuminate; these are eventually followed by pinnate leaves.

Brassaiopsis Decne. & Planch.

(*Wardenia* King, syn. nov.)

The genus *Wardenia* with its single species *W. simplex* King has been found so far only in a few localities in Perak and Selangor and hitherto has been considered monotypic. F. R. I. Kepong Herbarium has several specimens of *Wardenia simplex* King, the type species of the genus cited below. These collections supplement the original from Ulu Kerling, Perak, made by Kunstler over 80 years ago.

Two collections made in 1955 and 1969 in Trengganu, appear to represent a second species of this genus. It is described as a 'fleshy treelet' and differs from *W. simplex* in several obvious features, its elliptic acuminate cuneate (rather than ovate subcordate) leaves, much shorter and more slender petioles, and diminished inflorescence with little if any branching, and perhaps its longer pedicels and sparser puberulence. The material is rather incomplete; no fruits are available. The flowers are evidently past anthesis and the ovaries starting to enlarge. They clearly show a bilocular ovary, each cell with a single ovule. This conflicts with King's original generic description of *Wardenia* which calls for a unilocular ovary that develops a dissepiment later, separating the seeds, but agrees with the diagnosis of *Brassaiopsis*. According to Philipson (Bot. J. Linn. Soc. 63, Suppl. 1: 90, figs. 1–6. 1970) the original observations may have been wrong as the type collection definitely has 2-locular young fruits. The floral character of "ovary 1-celled. 2-ovulate" should be treated with caution, however, as in any case it 'disappears' in the fruit phase which is more normal for Araliads, i.e. there is one seed per loculus. The ovular character may not differ therefore from the situation in

Brassaiopsis Decne. & Planch. (including *Euaraliopsis* Hutchinson, which is *Araliopsis* Kurz non Engler). It would appear that *Wardenia* differs from *Brassaiopsis* only in having simple leaves. However, simple-leaved species of *Brassaiopsis* have already been described. Philipson (1951)* for example describes *B. castaneifolia* from Burma, which has simple leaves. Thus the generic distinction does not appear to be tenable. The venation pattern in the simple-leaved species is quite easily reconciled with that of the compound or palmately lobed-leaved species.

In both *B.* (*Wardenia*) *simplex* and *B. minor*, and in *B. polyacantha* and *B. elegans*, the young parts are covered with a rufous furfuraceous indument. Microscopic examination reveals that this is made up of numerous slender brachiate to stellate hairs with a variable number of branches and considerable variation in size. These structures are more or less ephemeral and the stems, leaves, etc., become glabrescent with age. These hairs are virtually identical in all four species, though their abundance varies. They are densest on the innovations and buds of *B. polyacantha*.

The sheathing base of the petiole and the adnate stipules are similar in all four species. The petiole base is obliquely invaginated and the basal margins abruptly produced into a pair of lobes at a certain distance away from the base, as in shown in the accompanying figures. This pattern also shows up in the lowest inflorescence bracts, which appear to be much modified leaves with the blade and petiole reduced effectively to the sheath and ligule, although a prolongation representing the blade (and showing lateral nerves) but tightly cylindrical-subulate, may be present.

The venation patterns in the leaves of all four species is comparable; the lowest lateral nerves are always inserted on the midrib by means of an outcurved junction. They are elevated beneath. There are comparatively few, i.e. widely spaced secondaries often with subparallel intermediate nerves between them. The lowest pair of lateral nerves tends to run up at or very near the blade margin and justifies the term 'subtriplinerved'. In the palmate-leaved species these nerves give off leaflets which are thus asymmetrical. The overall veining pattern is camptodromous.

Consideration of these further characters, indument, petiole-ligule-stipules, and veining, adds weight to the decision to reduce *Wardenia* to *Brassaiopsis*.

In R. Viguier's anatomical study of Araliaceae (1906) *Brassaiopsis* was included (in the 'Shefflerineés' p. 96) and a characterization of its petiole anatomy was presented (the species not specified). For *Wardenia*, Viguier apparently had no material and he was unable to compare it anatomically with other genera. (He expressed doubt that it pertained to Araliaceae and suggested that it might belong to the Cornaceae). However, such doubt is unnecessary and it is preferable to reduce *Wardenia* to the status of a synonym of *Brassaiopsis*. This is also the view of D. G. Frodin (Misc. Rec. Fl. Mal. Found. III: 8, 1973).

KEY TO MALAYAN SPECIES OF BRASSAIOPSIS

1. Leaves palmately lobed or divided
    2. Leaves palmately 5–9-lobed, large to very large, to 60 cm wide; small trees .... *B. polyacantha*
    2. Leaves digitate with 3 or 5 or up to 3 leaflets, medium, to 25 cm. wide.
        3. Leaflets 3–5; inflorescence branches with terminal umbel and a few lateral ones .... *B. elegans*
        3. Leaflets 5–9; inflorescence branches racemose-umbellate .... *B. glomerulata*

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* Philipson, W. R. 1951. Contrib. to our knowl. of Old World Araliaceae. Bull Brit. Mus. (N.H.) Bot. 1 (1): 1–20.

1\. Leaves simple.

4\. Leaves ovate-subcordate, to 35 cm long or more; petioles stout elongate, 15 cm long, 5 mm thick. .... *B. simplex*

4\. Leaves elliptic, cuneate at base, smaller, to 25 cm long; petiole to 7 cm long, 2 mm thick .... *B. minor*

ENUMERATION OF MALAYAN SPECIES OF BRASSAIOPSIS

1\. **Brassaiopsis polyacantha** (Wall.) Banerjee, Indian Forester 93: 341. 1967. *B. palmata* Kurz, J. As. Soc. Bengal 39, 2: 77. 1870. King, Mat. Fl. Mal. Pen. in J. As. Soc. Bengal 67: 61. 1898; Ridley, Fl. Mal. Pen. 1: 887. 1922.

Malayan collections: KEDAH: Gunong Inas F. R., Sg. Kepang, alt. 3000 ft., tree 40 ft. tall, 3 ft. girth, fruit faintly bluish with white spots, in terminal raceme 2ft. long, 7.2.1968, *Whitmore FRI-4639* (KEP); *FRI-4644* (KEP). — Ulu Pantai Mulik, 22.3.1938, *Sow KEP-34612* (KEP). PAHANG: Cameron Highlands, Gunong Brinchang, alt. 6000 ft., 4.5.1964, *M.E.D. Poore KLU-8126* (KLU) — Telom Valley, 21.8.1931, *Jaamat KEP-25199* (KEP). — Bukit Tinggi village, Bentong Rd., tree 30 ft., 8.2.1966, *Kochummen KEP-97777* (KEP). — Bentong Rd. between Genting Sempah and Bukit Tinggi, alt. 1500 ft., 21.12.1968, *Stone 8319* (KLU). — Bentong Rd. just beyond Genting Sempah, 1800 ft. alt., 2.2.1968, *Whitmore FRI-4623* (KEP). PERAK: Maxwell Hill Road, 5½ miles, 29.10.1969, *Kochummen FRI-2860* (KEP),

Poore 8126 differs in having more coriaceous leaves, appressed stellate hairs, thornier petioles. It may be a different species.

2\. **Brassaiopsis glomerulata** (Bl.) Regel, Gartenfl. 12: 275. 1863. *B. speciosa* Decne. & Planch. Rev. Hort. 4, 3: 106. 1854. *Hedera glomerulata* Blume, Bijdr. 1: 872. 1826. — *Aralia glomerulata* (Bl.) DC. Prodr. 4: 265. 1830.

Distribution: From India and S. W. China to Malaysia, Sumatra, and Java.

MALAYA: PAHANG, *I. H. Burkill & R. E. Holttum SF-7882* (SING); s.n. in 1922 (SING). NEGRI SEMBILAN, *Md. Nur SF-11729* (SING).

This species may be recognized by its stature, for it becomes a tree up to 10 m tall; by its distinct (petiolulate) leaflets; and by the long inflorescence branches bearing umbellules of about 25–35 flowers.

3\. **B. simplex** (King) B. C. Stone, **comb. nov.** *Wardenia simplex* King, Mat. Fl. Mal. Pen. in J. As Soc. Bengal 67: 60. 1898. Ridley, Fl. Mal. Pen. 1: 887. 1922. — Fig. 3.

MALAYA: PERAK, Slim Hills F. R., ridge top, 2500 ft. alt., unbranched small tree 15 ft. tall, trunk with distant thorns, inflorescence terminal, 4 Sept. 1966, *Whitmore FRI-794* (KEP). SELANGOR, Compt. 12, Chadangan F. R., Ulu Selangor, hill forest, 1200 ft. alt., tree 10 ft. tall, girth 4 in., 27.9.1966, *Chelliah KEP 98147* (KEP).

4\. **B. elegans** Ridl. Fl. Mal. Pen. 1: 888. 1922. — Fig. 4.

MALAYA: PAHANG; Cameron Highlands, *J. Wyatt-Smith s.n.* (KEP). SELANGOR: Genting Sempah Ridge trail, 2500 ft. alt., 11.11.1970, *Stone 9578* (KLU).

5\. **Brassaiopsis minor** B. C. Stone, **sp. nov.** — Fig. 5.

Arbuscula, ramulis 5 mm diametro. Folia simplices elliptica marginibus in partem mediam distalem serratis; petiolo 6–8 cm longo c. 1.5–2 mm diametro basi breviter vaginantio; lamina tenue coriaceo basi subtriplinervio nerviis c. 6–8

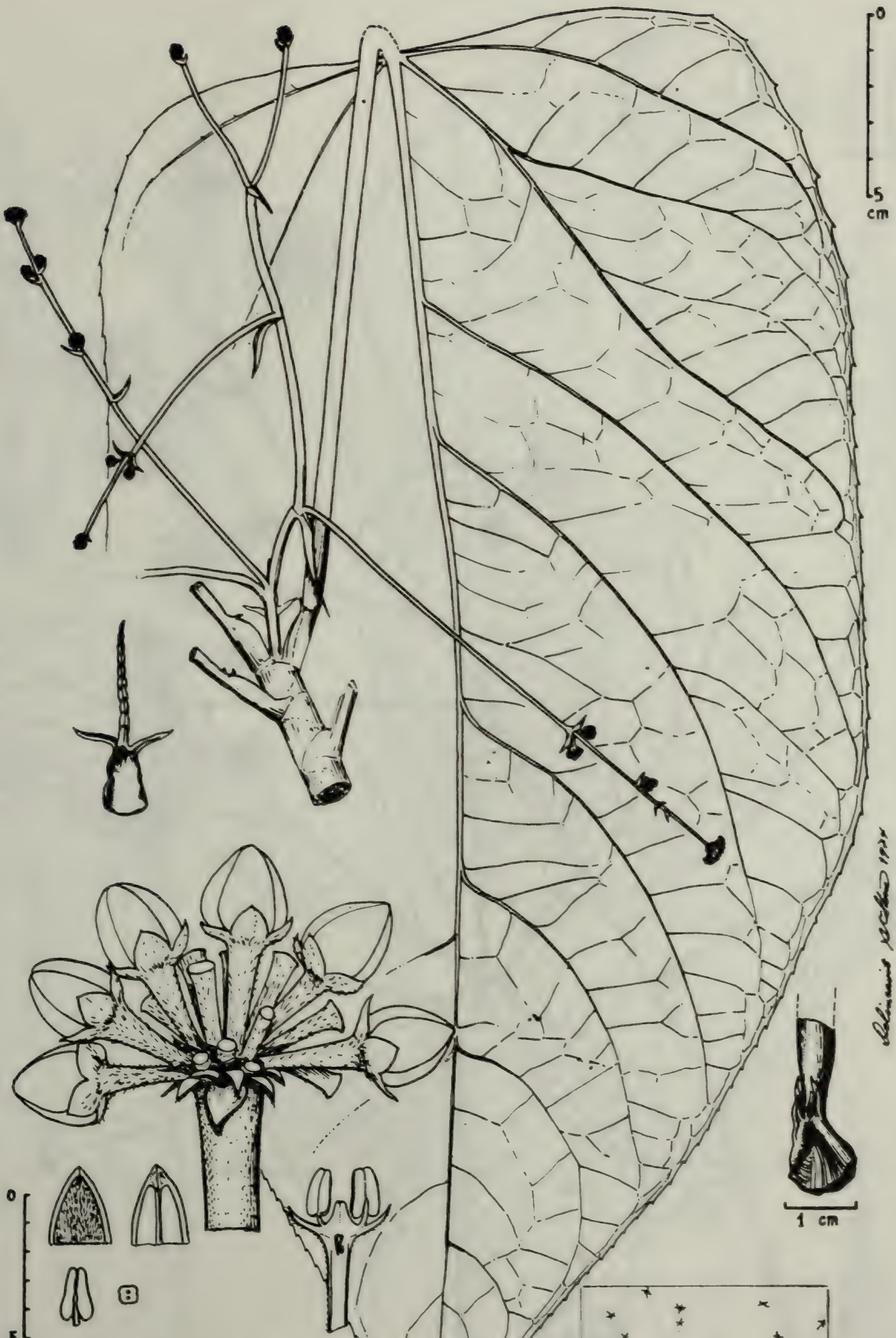

Fig. 3. *Brassaiopsis simplex* (King) Stone. (*Wardenia simplex* King). Leaf. inflorescence, floral details, stipule detail, pubescence. *FRI-12741.*

Fig. 4. *Brassaiopsis elegans* Ridl. Leaf, inflorescence, floral details. *Stone 9578.*

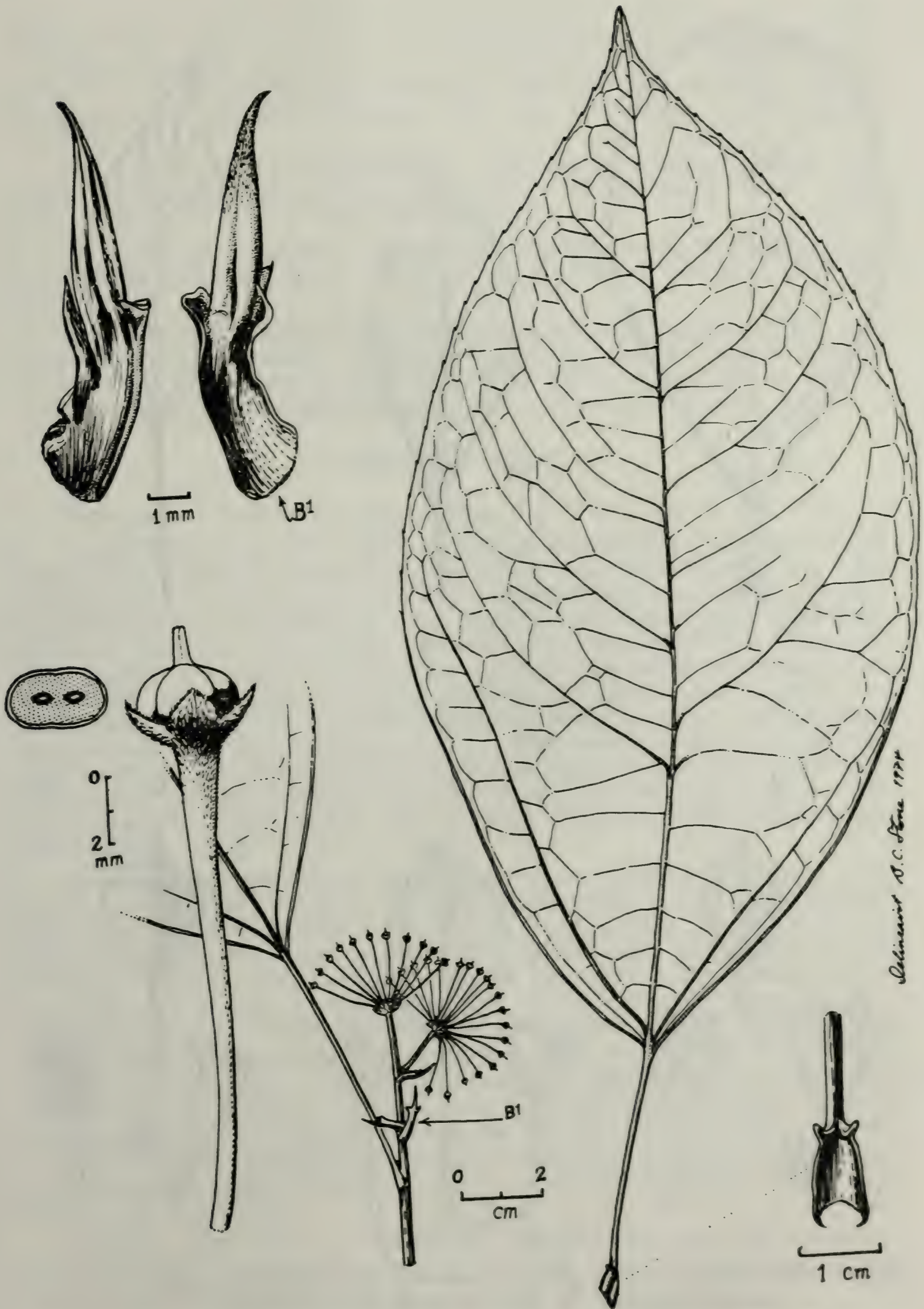

Fig. 5. *Brassaiopsis minor* Stone. Leaf, stipules, bracts (left: dorsal, right: ventral), inflorescence, and floral details (B^1:— the lowest inflorescence bract with a stipular-ligulate base). Type collection.

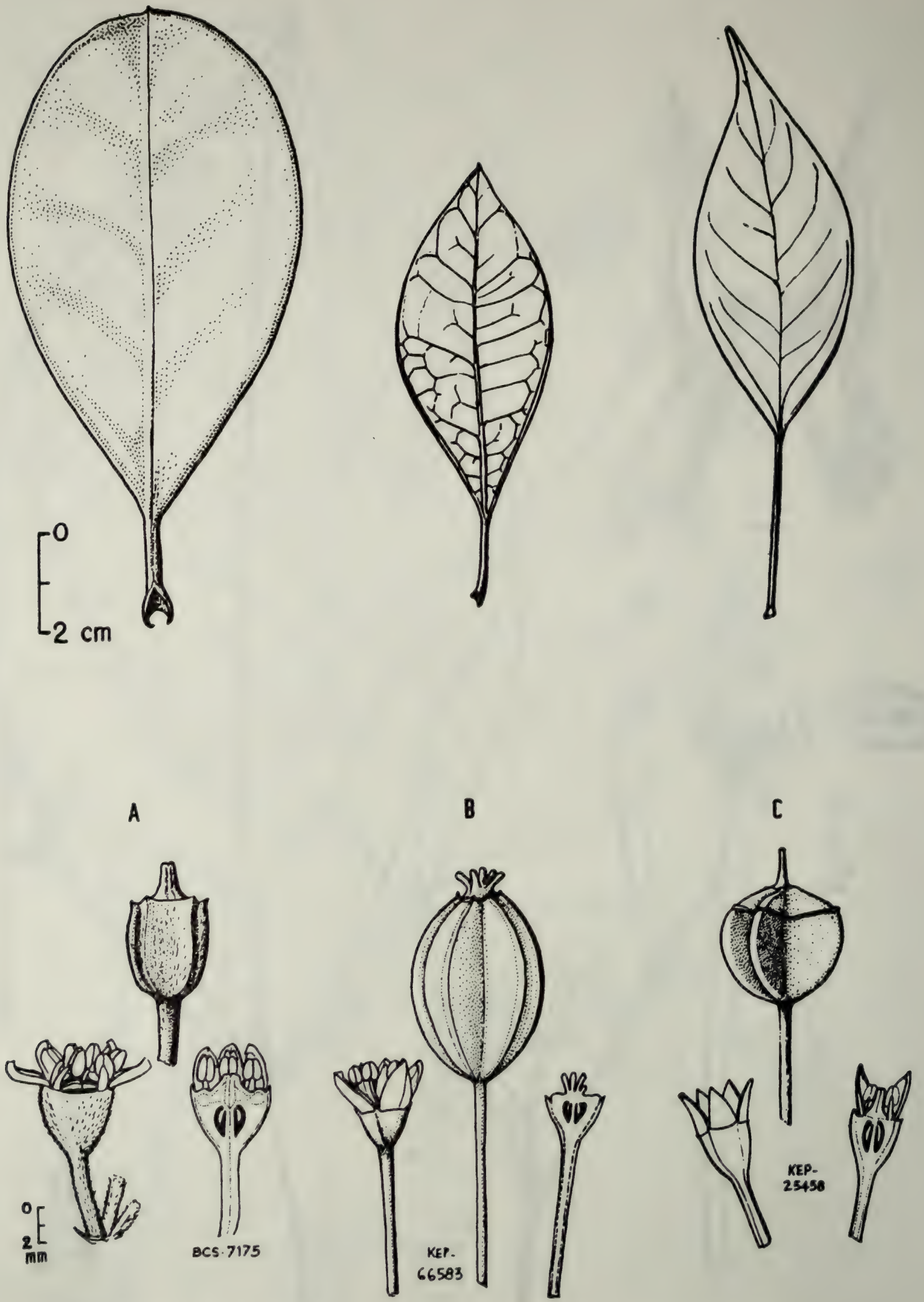

Fig. 6. Comparison of *Schefflera singularis* Stone with two *Dendropanax* species.

A:—*Schefflera singularis,* leaf and floral details, type collection.

B:—*Dendropanax maingayi* King, leaf and floral details, *KEP 66583.* and fruit, *Poore 1072.*

C:—*Dendropanax lancifolius* Ridl. cfr., leaf and floral details, *Symington 25458.*

paribus, usque ad 25 x 12 cm, apicem versus abrupte acuminato, basi cuneato. Inflorescentia terminalis, brevis, 4–5 cm longis, bracteatis, pauci-vel non-ramosis, umbellatis; bracteolis deltoideis c. 1–1.5 mm longis rufo-puberulento-ciliolatis; pedicellis c. 15 mm longis; calyce 5-dentato; ovario rotundato-lobulato, depresso, biloculare, stylis binis unitis columna 1 mm longo formantibus. Loculi ovarii 2, uniovulati.

Holotype: MALAY PENINSULA: TRENGGANU, Gunong Pahang, Ulu Brang, camp 3, humid deep valley on granite; alt. 3500 ft., fleshy treelet, flowers white; 21.9.1969, *Whitmore FRI-12741* (KEP).

Additional spec. examined: TRENGGANU: 34th mile, Kuala Trengganu, Besut Rd., lowland forest, (W. side), woody 2′ high, 8.9.1955, *J. Sinclair & Kiah SF-40775* (SING).

This is another simple-leaved species of *Brassaiopsis*. Originally I had considered it as a new *Wardenia*. The flowers show clearly that the ovary is bilocular and there is a single ovule in each loculus. The slender shorter petioles, elliptic-cuneate leaves and shorter inflorescence quickly distinguish this from *B. simplex*.

Hederopsis King

Type species: *Hederopsis maingayi* King, Hk. Fl. Brit. Ind. 2: 739. 1898.

Originally described from rather inadequate material, this genus (endemic in Malaya and apparently Sumatra, monotypic) has in the last few years been collected rather widely and is in fact locally common in a few localities. It has been suggested by Frodin that the genus could be merged with *Macropanax* Miq. which appears to differ only in its usually 2-3-locular ovary, this structure in *Hederopsis* being normally 5-6-locular. The difference is a slight one, but King's genus can be retained for the time being until a broader-based comparison can be made. The leaves are palmate-digitate, often with 5 leaflets, or with 3, or even 4, and sometimes (on flowering branches) reduced to 1 leaflet. The slender petioles may reach a length of 56 cm, and the terminal leaflet (always slightly longer than the laterals) a length of 31 cm and a width of 12 cm. The margins are dentate with small rather distant teeth. The petiolules may reach a length of 15 cm (again shorter on the lateral leaflets). — Fig. 7.

The spirally disposed leaves have a rather short sheathing base about 1 cm long or less; when very young the margins are ciliate with pale brown multiseptate hairs, which are often laterally adnate in flat 'bundles'. The juvenile stems are similarly rather densely hairy, but the hairs are ephemeral and all mature and submature shoots are glabrous. The base of the inner surface of the sheath shows a purplish spot adjacent to the axillary bud. The bud is compressed, purplish, pubescent, and bears 2 imbricate minute prophylls (which are more or less deltoid when flattened); these are equivalent to the leaf-sheath and show the ciliate margin and, often, a more or less produced apical elongation sometimes bearing three tiny lobes (suppressed leaflets). The outer face is usually rather pubescent. Similar prophylls occur on the terminal shoot in the uppermost region during renewed growth following the resting period, which is evident from the succession of several long internodes followed by a short series of very crowded internodes on the main branches and leafy shoots.

Individual plants of this species become attractive small trees with a rounded crown, the trunk sometimes exceeding 90 cm girth, often fluted at base, giving off a few main branches; the whole tree may reach 15–20 m height.

In Ulu Langat (Selangor) above the Reservoir (Ponsoon) there are several of these trees, copiously fruiting in January-February 1975. The fruits are subglobose and still green when ripe.

Fig. 7. *Hederopsis maingayi* King. Leaf and floral details, and fruit.

Spec. examined: MALAY PENINSULA: KEDAH: Ulu Muda Forest Reserve, Compartments 115 & 116, 1500 ft. alt., a tree 40 ft. high, girth 24″, bole fluted, with small buttresses, bark rugose, lenticellate, inner bark thick brown, with watery exudate, wood white, fruits green. 21.1.1969, *Y. C. Chan FRI-6782* (KEP). PERAK: Bintang Hijau F. R., secondary forest, tree 50 ft. tall, 26″ girth, flowers pale yellow, faintly aromatic, cut bark smelling of resin, bole slightly fluted, 22.11.1966, *Rahim Ismail KEP-98531* (KEP). KELANTAN: Ulu Sungei Lebir Kecil, 500 ft. alt., 17.9.1967, *P. F. Cockburn FRI-7123* and *7123* (KEP). SELANGOR: Ulu Langat, 2 miles from Kg. Injin Satu, tree 50 ft. high. 17.4.1963, *Abdul Samat 196* (KIU). — Ulu Langat Forest Reserve, tree 30 ft. high. 9.3.1966 *Whitmore FRI-106* (KEP). — Ulu Langat, Bukit Lakwak, Kg. Panson, n.v. (Temuan) "Kayu pacha" 4.10.1958, *Gadoh, Phytochem. Survey 1015* (KEP). — Ulu Langat above NEB works, stream valley, tree 10 m x 35 cm, fruits green, 7.2.1975, *M. M. J. van Balgooy & B. C. Stone 2249* (KLU etc.). PAHANG: Ulu Tembeling, lowlands, 28.5.1931, *Henderson SF. 24550* (SING). — Ulu Gali, Raub, 27.9.1929, *Kalong KEP-20274* (KEP). — Cameron Highlands, K. Mensum to Boh Estate, 24.9.1971, *H. S. Loh FRI-17399* (KEP). — Same locale, 3.3.1972, alt. 2000 ft., tree 40 ft., girth 30″, *Y. C. Chan FRI-19932* (KEP).

Schefflera J. R. & G. Forst.

Schefflera singularis B. C. Stone, sp. nov. — Fig. 6A.

Liana glabra innovationibus inflorescentiaque excepto, pilibus perminutis stellato-quinque-brachiatis; ramis usque ad 1 cm diametro teretibus cortice griseo; ramulis foliaceis usque ad 6 mm diametro in sicco longitudinaliter canaliculato-ruguloso; foliis simplicibus elliptico-obovatis marginibus valde sed anguste revolutis apice obtusis vel minute apiculatis vel rotundatis vel retusis, basi cuneatis, rigide percoriaceis costa in canaliculo costali utrinque leviter elevato, nerviis invisibilis; petiolo 5–20 mm longo. 1.5– mm crasso in sicco ruguloso basi ligulato ligulo 5 mm longo marginato; lamina 2–12 cm longo 1.5–6 cm lato apiculo 0.5–2.5 mm longo vel nullo; nerviis lateralibus c. 5–7 paribus sed omnino obscuris, nerviis basalibus marginam formantibus. Inflorescentia terminalis bisumbellatis (composito-umbellatis) usque ad 3 cm longis axibus griseo-albide furfuraceis demum glabrescentibus bracteis deltoideis c. 4 mm longis bracteolis c. 1–2 mm longis scarioso-ciliato-marginatis. Umbellae c. 5–10-floriferae, pedicellis c. 4 x 0.8 mm, calyce obconico 3 x 3 mm margine obscuriter 5-dentato minutissime ciliolulato, petalis 5 deltoideis 2 x 1.8 mm intus obscuriter carinatis apicibus unguiculatis, staminibus 5 filamentis albidis c. 1 mm longis antheris submedifixibus ovatis 1 mm longis erectis, disco leviter elevato, stylopodio late conico truncato vix 1 mm alto 2 mm lato, stigmatibus 5 obscuris radiatis ad apicem stylopodii sessilibus. Fructus immaturis glabratus obconico-turbinato-hemiglobosus 5 x 4 mm calyce undulato alte-marginatus stylopodio centrale 1 mm alto.

Holotype: MALAYA: PAHANG, Gunung Ulu Kali, summit area, 5000-5800 ft. alt., elfin forest with Dacrydium, big shrub with thick brittle leaves pale tawny-greenish beneath, 23.7.1967, *B. C. Stone 7175* (KLU).

Other specimens examined: MALAY PENINSULA, PAHANG, Gunung Ulu Kali, summit area, shrub in mossy forest, 19 Sept. 1967, *J. Dransfield KLU-8068* (KLU); same location, 27.6.1971, *Mahmud b. Sidek* and *W. R. Stanton KLU-16312* (KLU). Ginting Highlands Rd. 4.5 miles (c. 3000′), 12.6.73, *Mohd. Shah & Md. Ali MS. 2987* (climber? — fls. dark green in bud), (SING). Isotypes in *L* and *KLU*.

This very distinct endemic species so far has been collected only on the summit area of the mountain Gunung Ulu Kali, in the Ginting Highlands of Pahang, on the Selangor border. At first it was considered to be a new species of *Dendropanax* but after much discussion and hesitation it is here described as a *Schefflera*. In nearly all features this species agrees with the formal definition of a *Dendropanax*, but differs in having a perceptible though limited ligular process at the base of the petiole, similar to that in at least most Scheffleras. In addition the exceedingly coriaceous leaf, with virtually invisible venation, appeared inconsistent with the condition in *Dendropanax*, which at least in the Malaysian species, is characterized by rather evident and subtrinerved leaves, as may be seen in *D. maingayi* and *lancifolius*, illustrated in Fig. 6 B and 6 C. *Schefflera singularis*, as shown in Fig. 6 A, not only has invisible nerves and evident stipular ligule, but a more oboval laminar shape than the two species of *Dendropanax*. Nonetheless, in floral characters there is almost no difference between the new *Schefflera* and the two Malayan *Dendropanax* species, as the figures cited also display.

Within *Schefflera* the vast majority of species possess compound leaves with trifoliolate or palmate leaflet arrangements. Rarely, as in *Schefflera lanceolata* Ridl., simple leaves occur, though even in this species older branches may show trifoliolate leaves. Another such example is *Schefflera simplicifolia* Merr. of the Philippines. Among Malesian species I know of no other similar cases, though they may occur. Thus *Schefflera singularis* stands apart from nearly all other Malayan Scheffleras by its simple leaves.

Another difference lies in the form of the inflorescence, which in *Schefflera* is usually a compound umbel, i.e. an umbel of umbels or umbellules, while in *Dendropanax* the umbel is often simple; but there are also species of *Dendropanax* with compound umbels.

The genus *Schefflera* includes species which are climbers, others which are shrubs or trees, the latter often epiphytic. *Dendropanax* species are apparently mostly shrubs or trees. *Schefflera singularis* is a high-climbing woody liana.

A comparison of generic diagnoses in such standard works as various floras, treatise* on the Chinese Araliaceae (Sargentia 2. 1942), and Vol. 2 of Hutchinson's "Genera of Flowering Plants" (1967), does not appear to reveal any completely dependable differential features to distinguish *Schefflera* from *Dendropanax* except perhaps the presence of a developed stipular ligule. The degree of connation or separation of the style-tips seems to be highly variable within *Schefflera* and not a diagnostic character.

In the light of these facts it is evident that further work is necessary to clarify the distinction between *Dendropanax* and the small number of *Schefflera* species with predominantly simple leaves. One may in fact question whether *Dendropanax lancifolius* Ridl. is not itself misplaced in *Dendropanax*. (In passing it may be noted that the generic name *Dendropanax*, although treated as neuter by the original authors, has usually been considered masculine in gender, and thus the epithet is spelled here *lancifolius* rather than *lancifolium* as it appears in Ridley's Flora).

Acknowledgements

It is a pleasure to record the debt owed to Prof. W. R. Philipson of the University of Canterbury for stimulating discussions concerning Araliaceae and for his several suggestions which have improved and augmented this paper. I am also grateful to D. E. Frodin, University of Papua New Guinea, and Prof.

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* By H. L. Li.

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Reference

Philipson, W. R. 1970. The Malesian species of *Gastonia*. *Blumea* 18: 490–495.

A Note on the Cytology of *Botrychium lanuginosum* and the Occurrence of the Genus in Malesia

by

A. C. JERMY* and T. G. WALKER**

Summary

Over the past twenty-five years intensive plant collecting has shown two species of *Botrychium* (*B. lanuginosum* Wall. ex Hook. & Grev. and *B. australe* R. Br.) to be present in eastern New Guinea, the former hitherto confined to Central—S.E. Asia and reaching to the Central Himalaya and the latter Australasian with a possible representative in S. America. A further species, *B. daucifolium* Wall. ex Hook. & Grev., is distributed from Sri Lanka (Ceylon) to the Philippines and Sulawesi (Celebes) with questionable outlying records in Fiji and Samoa, reaching S. China in the North, and replaced by a taxon of doubtful specific identity in Japan (*B. japonicum* (Prantl) Underw.). *B. lanuginosum* was found in large quantities in the kunai grasslands at 1600 m in the Finisterre Mountains of E. New Guinea and material fixed in the field has proved to be octoploid n = 180) and also hexaploid, suggesting the tetraploid cytotype recorded by other workers in India and Sri Lanka may also be present in New Guinea.

INTRODUCTION

The appearance of *Botrychium* in S.E. Asia and Malesia is seasonal. Its ecological requirements are little known but its appearance may be linked with the increased rainfall seen just before the full monsoon develops. For this reason limited collections have been made as the aerial parts of the leaf quickly become yellow and die down after the spores are shed. Three species have so far been recorded in Malesia, *B. lanuginosum* Wall. ex Hook. & Grev., *B. daucifolium* Wall. ex Hook. & Grev. and *B. australe* R. Br. The first and last species are components of well drained soil in the open anthropogenic grasslands in Malesia (from 1600 — 2700 m in New Guinea) and on similar grassy banks or more rarely in woods on the Asiatic mainland. *B. daucifolium* is a species of more shady situation often in open woodland in the Himalaya and on the open floor of the rain forest in Borneo and Sulawesi. Betty Molesworth Allen (1959) discovered a colony at 1500 m on Gunong Perdah in an opening in the tall forest, growing in a scrub of *Didymocarpus* and young *Cyathea.* She records the soil as being a black sticky humus.

KEY TO MALESIAN SPECIES OF *Botrychium*

1 Fertile segment arising from the rachis of the sterile blade, ± equal in length to adjacent sterile pinnae .... 1 *lanuginosum*

1 Fertile segment arising from the petiole below the sterile blade; the stalk of the fertile segment 1 — 2 times as long as the sterile blade

  2 Fertile stalk ± equalling sterile blade; upper pinnae linear-lanceolate or triangular, pinnatifid or dentate only .... 2 *daucifolium*

  2 Fertile stalk at least twice as long as the sterile blade; upper pinnules ovate, deeply cut to costa .... 3 *australe*

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1 *B. lanuginosum* Wall. ex Hook. & Grev. *Icon. Fil.* tab. 79 (1829).

The name first appeared in Wallich's Catalogue of 1828 without a description and was described by Hooker, the figure by Greville (*l.c.*) drawn from material supplied by Wallich. Ballard (1940) discusses the typification and describes the specimen in Greville's herbarium at the Royal Botanic Garden Edinburgh from which the two lower pinnae were removed, thus giving rise to the abnormal plant seen in his plate 79.

The species ranges from the Central Himalaya across China to Taiwan, south to Sri Lanka on the Indian subcontinent and in Malesia to Luzon, Sumatra, Java and New Guinea. The species is distinct in having a broadly deltate tripartite sterile blade, the lobes usually 3–4 pinnatisect, and with the fertile scape arising from the rachis above the insertion of the two lower pinnae (see Figs 1 & 2). The bud, rachis and especially the costal axils are usually sparse to densely covered with long unbranched hairs although some fronds in the New Guinea population mentioned below were almost glabrous. Hayata (1914) has described the glabrous form as *B. leptostachyum*, later to be combined by Nakai (1925) as a variety of *B. lanuginosum*, but in view of the wide variation in the above population both are of doubtful status. The degree of dissection of the sterile blade varies, younger plants being usually less compound, but always more dissected than either *B. daucifolium* or *B. australe*. There is no apparent correlation between ploidy level and degree of cutting or size of sterile frond (see Figs 1 & 2).

2 *B. daucifolium* Wallich ex Hook. & Grev. *Icon. Fil.* 2, tab. 161 (1830).

Wallich (1828) listed the first gatherings of this (No. 49) as *B. subcarnosum* and later by the name Hooker took up for it. The specimen drawn is in the Edinburgh herbarium and other plants of the same gathering at the British Museum (Natural History) London.

The species ranges from a similar area in the central Himalaya east to Taiwan and south to Sri Lanka. In Malesia it is found throughout the archipelago to Sumbawa Is. (G. Batulanteh), Celebes (G. Bonthain) and Mindanao (Mnt Apo) and Negros (Cuernos de Negros). Allen (1959) found two populations in the Cameron Highlands area of Pahang. There are specimens in the Kew Herbarium from Upola, Samoa and Nadavivatu, Fiji which compare well with material of *B. daucifolium* from Asia, but a closer study of more recent material needs to be made.

B. daucifolium is distinct in having thin, but not membranous, lamina tissue and a less dissected frond in which the upper pinnae are barely cut (see Fig 3) but lobed with the segments toothed. The fertile spike arises from the petiole about 10 cm or more below the insertion of the blade and the fertile segments are strict, not spreading as in the other two species. The species varies in its hairness, some species in Borneo being quite densely pubescent on the rachis and costae. Allen (1959) mentions that the very young fronds on her Malayan plants were covered with copious pale hairs. Himalayan plants tend, in herbarium specimens at least, to be more glabrous, as do the adult plants of Allen, who gives a fine general photograph of the species (*l. c.* facing p. 251).

Material from Japan, E. China and some from Taiwan, being more membranous, more deeply toothed and with the fertile stalk somewhat longer, has been separated off as *B. daucifolium* var. *japonicum* Prantl, raised by Underwood

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Facing page

Figs. 1–4. Silhouettes of *Botrychium* 1 & 2. Silhouettes of *Botrychium lanuginosum* from Moro, Finisterre Range, New Guinea showing range of dissection. 1: *Jermy 3887* (× ¼); 2: *Walker 8333*, octoploid plant from same population (× ¼). fs = fertile spike. 3: *B. daucifolium* Gunong Dempo, Sumatra, *C. J. Brooks 15881* (× ¼). 4: *B. australe* Western Highlands District, New Guinea *J. S. Womersley*, NGF 15213 (× ¼).

(1898) to a species. It is certainly related in its morphology to the typical mainland asian *B. daucifolium*. A small form was described by van Alderwerelt van Rosenburg (1911) from Preanger Regencies, Java under the name of var. *parvum*. Later in 1913 the same author described yet another variety, *subbasalis*, which was not only smaller than usual for *B. daucifolium* but had the fertile spike arising towards the base of the stipe as in *B. ternatum* and *B. australe*. Clausen (1938) considered this, from the published description only, to be a possible new species. We have not studied van Alderwerelt van Rosenburgh's type and must reserve judgement but it is our experience that juvenile and depauperate Botrychiums can appear very abnormal.

3 *B. australe* R. Br. *Prod. Fl. Nov. Holl.*: 164 (1810).

Collected and described by Robert Brown from material from Tasmania and New South Wales. The specimen in the herbarium of the British Museum (Natural History) from Parametta, Port Jackson can be taken as typical but the specimen at Kew is more complete (it contains roots) and is best to be designated lectotype. The species ranges from South Australia to New Zealand and north into south Queensland where it was recorded as *B. ternatum* (Thunb.) Sw. by Bailey (1883). It differs from the latter in its dissection of the thicker lamina which has hyaline marginal cells.

The sterile leaf is 10–20 cm long, ternate, with the central leaflet larger and more compound. The upper pinnae of this leaflet are ovate and cut to the costa, the resulting segments glabrous, linear and dentate at the truncate apex; the tissue is fleshy and the lamina margin is made up of two to three rows of hyaline cells. The compoundly branched and spreading fertile segment arises in the lower half of the stipe to a height of 30 cm. (see Fig. 4).

The map in Fig. 5 shows the range of the species in Australia. Its presence in Papua New Guinea in the Southern and Western Highlands Districts is a logical extension of this range. It grows in high altitude anthropogenic grasslands (*Miscanthus-Themeda* associations) and around 2700 m in *Danthonia-Poa* grassland and *Cyathea* scrub and in two localities together with *B. lanuginosum*. The taxonomy of this australasian complex is little understood and is being reviewed by New Zealand workers at present and their results are awaited with interest.*

THE CYTOLOGY OF *B. lanuginosum* IN NEW GUINEA

Whilst collecting fern material for subsequent taxonomic and cytological studies in Madang District, east New Guinea in 1964 the authors showed children in Moro, a village at 1680 m at the head of the Gusap River in the Finisterre Mountains, an illustration of *Botrychium*. Within the hour the children returned with armfuls of *B. lanuginosum* collected from amongst the kunai (*Imperata* grass) on old garden sites. This is a good example of the dangers of this method of collecting easily recognisable but possibly rare species. Luckily this population could withstand such collecting and some 50 specimens were taken to show the range of variation. Seven specimens thus collected had meiotic material and were fixed in the field.

One specimen (*Walker 8333*) showed exactly 180 bivalents at meiosis (Plate I) and three others (*Walker 8332, 8334, 8336*) 270 chromosomes and hybrid meiosis. The base number for *Botrychium* is well established as 45 and thus these New Guinea specimens were octoploid and hexaploid respectively. This contrasts with other counts for the species from the Indian subcontinent where Verma & Loyal (1960) recorded n=90 in a Himalayan specimen and Ninan (1956)

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* Dr J. Braggins, University of Aukland, N.Z., is of the opinion (pers. comm., 1976) that the New Guinea specimens constitute a new subspecies.

recorded n=90 and 2n=180, also for N India; Manton and Sledge (1954) showed a similar situation in Sri Lanka (n=90). Hence all previous counts are at the tetraploid level. The fact that we have hexaploid material showing hybrid behaviour suggests that the tetraploid may also be present in New Guinea.

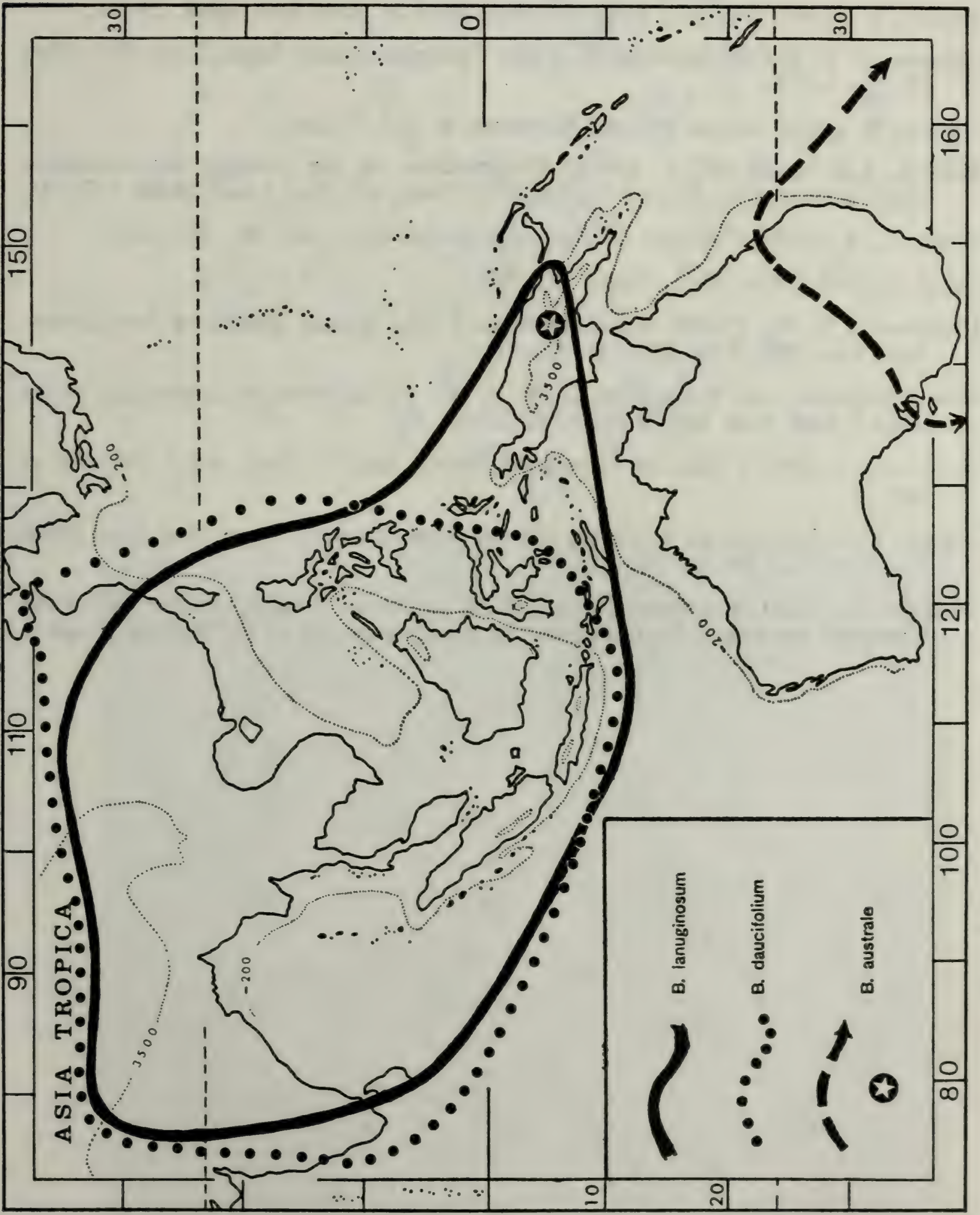

Fig. 5. Distribution of the three species of *Botrychium* found in Malesia.

REFERENCES

Allen, B. Molesworth (1959) Malayan Fern Notes. A preliminary note. Gard. Bull. Singapore **17**: 251–252.

Bailey, F. M. (1883) A synopsis of the Queensland Flora. Brisbane.

Ballard, F. (1940) Notes of ferns and fern allies II. Kew Bull. **1940**: 29–31.

Clausen, R. T. (1938) Monograph of the Ophioglossaceae. Mem. Torr. Bot. Club **19** (2): 3–177.

Hayata, B. (1914) Icones Plantae Formosae **4**: 134. Taipei.

Manton, I & Sledge, W. A. (1954) Observations on the cytology and taxonomy of the pteridophyte flora of Ceylon. Phil. Trans. roy. Soc. Lond. **283B**: 127–185.

Ninan, C. A. (1956) Cytology of Ophioglossaceae. Curr. Sci. **25**: 161–162.

Nakai, T. (1925) Bot. Mag. Tokyo **39**: 192.

Underwood, L. W. (1898) American ferns I. The ternate species of *Botrychium*. Bull. Torr. Bot. Club **25**: 521–541.

Van Alderwerelt van Rosenburg C. R. W. K. (1911) New or interesting Malay ferns 3. Bull. Jard. Bot. Buitenz. ser. 2 (**1**): 3.

——————— (1913) New or interesting Malay ferns 5. ibid. ser 2 (**11**): 6 et tab. 3.

Verma, S. C. & Loyal, D. S. (1960) Chromosome counts in some ferns from Naini Tal. Curr. Sci. **29**: 69–70.

Wallich, N. (1828) A numerical list of dried specimens of plants in the East India Company museum collected under the superintendence of Dr Wallich, London.

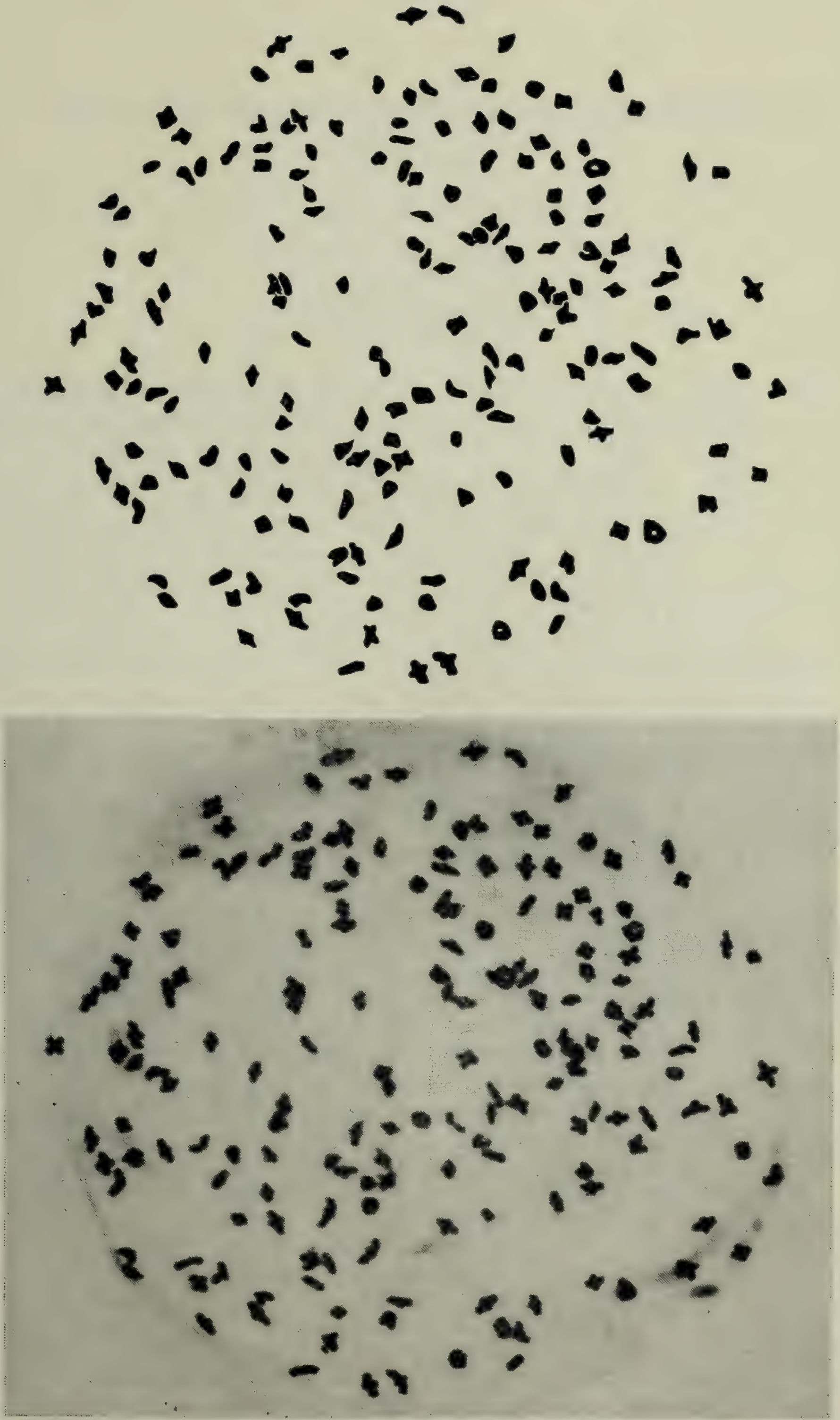

Plate 1. Permanent aceto-carmine squash of metaphase I of a spore mother cell of *Botrychium lanuginosum* (*Walker 8333*) together with explanatory diagram below. Magnification × 1000.

A Revision of the Malesian Species of Arthrophyllum Bl. (Araliaceae)

by

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The genus *Arthrophyllum* forms a well-defined group of species within the Araliaceae. Its principal distinctive characters are the single-celled ovary and the arrangement of the umbels on specialized flowering branches. The vegetative shoots bear pinnate or bipinnate leaves in spiral phyllotaxis. Branches do not develop until flowering occurs, when a terminal tuft of lateral branches develops. These bear opposite leaves of reduced size and terminate in a whorl of secondary branches which may themselves bear umbellules or which may branch again before doing so (fig. 1). Vegetative growth is continued by one or more innovations, with spirally arranged leaves, arising below the crown of flowering branches.

The geographical range of the genus almost coincides with that of Flora Malesiana, but extends slightly further west to the Nicobar Islands and northwards into Laos and Thailand, and the range does not include the Lesser Sunda Islands. Apart from the treatment in Ridley's Flora of the Malay Peninsula, no revision of the species has appeared. The many taxa given specific names by early investigators (most of which are here regarded as synonyms) were never critically compared, so that knowledge of the genus has remained confused and fragmentary and botanists have tended to avoid it. Consequently it has been found necessary to describe several new species, while at the same time reducing several others to synonymy.

The present revision is regarded as only tentative. Herbarium material is abundant, but most specimens are fragmentary and therefore fail to illustrate the unusual branch-systems which characterize some species. Specific distinctions seem to be unusually difficult to define on the basis of herbarium specimens, so that knowledge of the group will remain superficial until a comprehensive field study can be undertaken throughout the range of the genus.

The genus comprises two species-complexes, and also the anomalous *A. proliferum*. One of these complexes includes seven shrubby species with simpler inflorescences (no more than three degrees of branching), namely, *A. maingayi*, *A. montanum*, and *A. alternifolium* (from the Malay Peninsula, with the first species also from Sumatra and Borneo); *A. papyraceum* (from Sumatra); *A. pulgarense* and *A. cenabrei* (from the Philippines); and *A. kjellbergii* (from Celebes). The second complex consists of nine species of tree stature with larger inflorescences (having four degrees of branching). This complex occurs commonly throughout the range of the genus, and its subdivision into species presents considerable difficulty. To the east *A. macranthum* is abundant on the mainland of New Guinea, while on islands to the north a second species, *A. pacificum*, is recognized. In the Philippines and northern Moluccas this complex is represented by *A. ahernianum*, a species which also extends into the extreme north-east of Borneo. The complex is more difficult to classify further west and south, that is, in Celebes, Borneo, Java, Sumatra, and the Malay Peninsula. In the present

Fig. 1. *Arthrophyllum diversifolium*, diagrammatic sketch of habit showing vegetative and flowering branches (× 1/30).

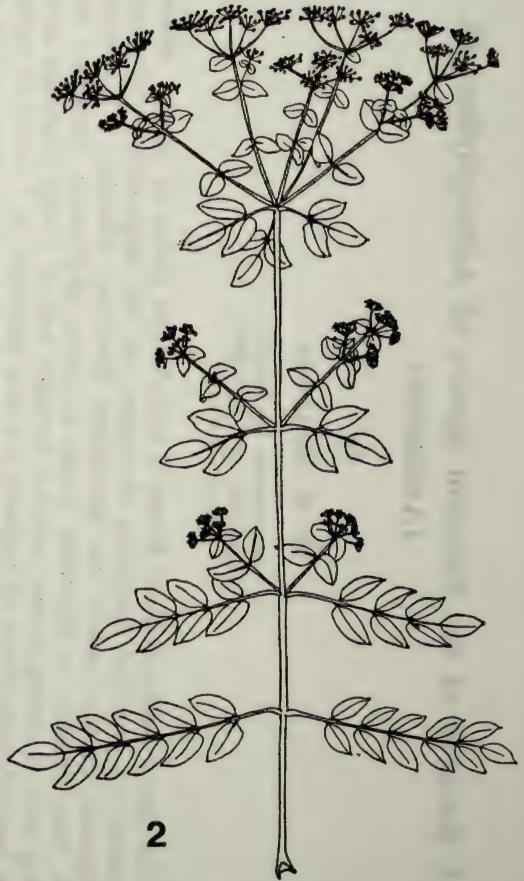


Fig. 2. *A. diversifolium*, schematic drawing of a single flowering shoot, with four degrees of branching (× 1/10).

revision, in addition to the widespread *A. diversifolium*, five entities from this area are given specific rank: three species endemic to Borneo (*A. crassum*, *A. collinum*, and *A. ashtoni;* one most distinctive species, *A. angustifolium*, which is rare in Borneo and the Malay Peninsula; and a species, *A. engganoense*, which is known only from the small island, Enggano, off the west coast of Sumatra. The remaining great mass of material is here treated as a single species, *A. diversifolium*. The variation and nomenclature of this widespread taxon is discussed separately under the section on that species.

ARTHROPHYLLUM

Arthrophyllum Bl. Bijdr. Fl. Ned. Ind. (1826) 878. *Mormoraphis* Jack ex Wall. Cat. n. 4931 (1831).

Sparingly branched trees or shrubs, unarmed. The leaves on vegetative shoots spirally arranged, imparipinnate, those on flowering branches often opposite, smaller, or reduced to a single leaflet; stipular sheath small. Inflorescence consisting of compound umbels, either solitary and terminal or more commonly borne on a cluster of specalized leafy branches arising from the axils of the uppermost leaves; pedicels not articulated. Flowers hermaphrodite; calyx an undulate rim; petals 4–6, valvate in bud; stamens 4–6, anthers curved, basifixed; ovary turbinate, 1-celled; disk fleshy, rising in the centre to the ± sessile capitate stigma. Fruit ovoid or spheroidal, often oblique; exocarp leathery; endocarp cartilaginous; seed solitary, pendulous; endosperm deeply transversely ruminate.

About 18 species (17 in Malesia) extending from the Nicobar Islands and in the larger islands or regions is as follows: Sumatra 4; Malay Peninsula 5; Java 1; Borneo 7; the Philippines 3; Celebes 2; Moluccas 2; New Guinea and Bismarck Archipelago 3. The genus *Eremopanax*, with several species in New Caledonia, may be congeneric.

KEY TO THE SPECIES ...

1\. a. Inflorescence becoming paniculate by the successive development of branches below the umbellules (figs. 3, 4) .... *1. A. proliferum*

b. Inflorescence a compound umbel 2

2\. a. Inflorescence with four orders of branching (fig. 2) 3

b. Inflorescence with three (or fewer) degrees of branching (figs. 5, 6) 11

3\. a. Leaflets lanceolate 4

b. Leaflets broader 5

4\. a. Leflets c. 4–7 cm long (fig. 12) .... *2. A. ashtoni*

b. Leaflets much longer .... *3. A. angustifolium*

5\. a. Pedicels (at early anthesis) ± 10 mm long 6

b. Pedicels (at early anthesis) c. 5 mm long, or shorter 7

6\. a. Peduncles of umbellules with bracts or bract-scars (fig. 13) .... *4. A. ahernianum*

b. Peduncles of umbellules (fig. 14) without bracts or scars .... *5. A. engganoense*

7\. a. Leaves associated with the umbels rotund (fig. 17) .... *6. A. collinum*

b. Leaves (or leaflets) associated with the umbels ovate or elliptic 8

8\. a. Leaves associated with the umbels ovate, ± fleshy, with the lower surface smooth (lateral veins obscure) (fig. 18) .... *7. A. crassum*

b. Leaves (or leaflets) associated with the umbels ± elliptic, coraceous or chartaceous, veins visible 9

9\. a. Young parts glabrous .... *8. A. pacificum*

b. Young parts with rufous tomentum 10

10\. a. Umbels at anthesis with numerous filamentous pedicels (fig. 15) .... *9. A. diversifolium*

b. Umbels at anthesis with fewer stout pedicels (fig. 16) .... *10. A. macranthum*

11\. a. Leaflets membranaceous or chartaceous 12

b. Leaflets coriaceous 14

12\. a. Mid-leflets about 16 cm long .... *11. A. papyraceum*

b. Mid-leaflets ± 8 cm long or shorter 13

13\. a. Leaflets usually 5–7 (fig. 7), primary inflorescence branches usually short (± 3–6 cm) and without articulations .... *12. A. maingayi*

b. Leaflets more numerous (fig. 10), primary inflorescence branches longer (10–20 cm) with one or more leafy nodes .... *13. A. kjellbergii*

14\. a. Leaflets c. 5 .... *14. A. cenabrei*

b. Leaflets more numerous 15

15\. a. Petals & stamens 6 .... *15. A. pulgarense*

b. Petals & stamens 4 or 5 16

16\. a. Leaflets 6 cm long, or longer (fig. 8) .... *16. A. montanum*

b. Leaflets shorter (fig. 11) .... *17. A. alternifolium*

1\. **Arthrophyllum proliferum** Philipson, *sp. nov.*

Arbor foliis imparipinnatis. Inflorescentiae ex suis propriis ramis natae, paniculatae factae ramis sub umbellulis iterum atque saepius ramificantibus.

Medium sized tree, glabrous. Leaves of the vegetative stems spirally arranged, imparipinnate, multijugate, 90 × 24 cm, of the flowering branches smaller with fewer pinnae or usually simple; leaflets obovate-oblong, c. 16 × 7 cm, chartaceous, margin entire, slightly revolute, base broadly cuneate to truncate, sometimes oblique, apex acute. Inflorescences terminating specialized plagiotropic shoots, bearing axillary flowering branches and ending in umbellules of a few flowers below which pairs of whorls of branches conitnue the growth of the inflorescence to produce an elongated panicle of umbellules.

Endemic to Papua New Guinea. Type: Territory of New Guinea, Morobe District, Mauwata Banda L.A., Bulolo, *Havel and Kairo NGF 17172* (Canberra).

In mid-mountain rain forest, reaching the canopy, on steep slopes, 300-1200 m.

The flower and fruit are typical of this well-defined genus, but the branching of the inflorescence is unlike that found in all other species.

Figs. 3–6. *3. A. proliferum;* a portion of inflorescence in the fruiting state (× ½); *4,* same, showing detail of ultimate branches of the inflorescence in the flowering stage (× 1). *5. A. maingayi,* terminal inflorescence (× ½). *6. A. montanum,* a single flowering shoot (× ⅓).

2. **Arthrophyllum ashtoni** Philipson, *sp. nov.*

Abor gracilis tomento fusco. Folia imparipinnata, foliolis lanceolatis vel late-lanceolatis, 3–7.5 × 1–2 cm. Inflorescentia ramis in proporium officium mutatis et in coronam terminalem dispositis, quarter ramificantibus.

A slender small tree, to 5 m high, young parts with brown scurfy tomentum. Leaves of the vegetative stems spirally arranged, imparipinnate, multijugate, to about 30 cm long; of the flower-bearing branches smaller with fewer pinnae, or simple; leaflets lanceolate to broadly-lanceolate; 3–7.5 × 1–2 cm, thinly coriaceous, margin entire, revolute, base broadly cuneate, apex tapered to sub-caudate, veins channelled above, visible below. Inflorescence a terminal cluster of specialized leafy branches; the main rays variable in length in the same inflorescence, ending in a whorl of secondary rays subtended by simple leaves; the secondary rays 4–12 cm long, bearing simple leaves, usually in an opposite pair and terminating in compound umbels; umbellules with about 8–10 flowers pedicels 4–10 mm long, furfuraceous.

Endemic to Borneo. Type: Brunei: Pagon ridge, *Ashton Brun 2341* (Kew).

Moss forest on sandstone ridge, and Kerangas forest, 1000-1550 m.

The small narrow leaflets are very distinctive. No other species with small leaflets has inflorescences which branch to the fourth degree.

3. **Arthrophyllum angustifolium** Ridley in Journ. Fed. Mal. St. Mus. 10 (1920) 136.

A shrub or small tree, 5 m high, young parts rufous tomentose, becoming glabrous. Lower leaves spirally arranged, imparipinnate, multijugate, about 70–90 × 30–40 cm; upper leaves reduced mostly unifoliate, opposite, broader, with petioles about 2–4 cm long; leaflets coriaceous lanceolate, c. 15–22 × 1.5–2.5 cm, tapering to an acute or obtuse apex, base cuneate, margin entire, slightly revolute. Inflorescence a terminal cluster of specialized leafy branches; the main rays 30 cm (or more) long, bearing simple leaves in opposite pairs ending in a whorls of c. 10–12 secondary rays subtended by simple leaves; the secondary rays 8–12 cm long, terminating in an umbel of 5–12 tertiary rays c. 2–3 cm long, each bearing an umbellule of c. 8–12 flowers, pedicels c. 5 mm long.

Malay Peninsula and Borneo. Type: Perak, Gunong Keledang, *Ridley 9683* (SING).

Occurs in forest and old regenerated forest on peat swamp at low altitudes or on ridges.

The lanceolate leaflets are unlike those of any other species. The grey bark is minutely fissured and bears many small orange lenticels. The wood is soft and white. The Peninsular and Bornean specimens are similar, except that the flower buds are larger in the Brunei plant.

4. **Arthrophyllum ahernianum** Merr. in Philipp. Journ. Sci. 1 (1906) Suppl. 109. — "*A. pinnatum* Clarke" F. -Vill. Novis. App. (1880) 103 — *Macropanax sp.* Vidal Rev. Pl. Vasc. Philip. (1886) 145. — *A. sablanense* Elmer in Leafl. Philipp. Bot. 1 (1908) 331. — *A. borneense* Merr. in Univ. Calif. Pubs. Bot. 15 (1929) 231, non Baker. — *A. elmeri* Merr. in Webbia 7 (1950) 319. — *A. merrilliana* Furtado, in Gard. Bull. 19 (1962) 185.

Tree up to 15 m high, young parts with rufous tomentum. Leaves clustered at the ends of the branches, spirally arranged on the vegetative shoots, imparipinnate, multijugate, articulated at the insertion of the pinnae; up to 200 × 60 cm; of the flower-bearing branches smaller with fewer pinnae, or simple; leaflets ovate-oblong, occasionally oblong-lanceolate, up to 35 × 12 cm, membranaceous or chartaceous, margin entire, revolute, base cuneate to rounded, usually oblique, apex short accuminate. Inflorescence a whorl of specialized leafy branches forming a terminal crown; the main rays up to 150 cm long (or more), bearing pinnate leaves usually in 1–2 opposite pairs, ending in a whorl of secondary rays up to 30 cm long terminating in compound umbellules; umbellules with about 10–20 flowers; pedicels c. 10 mm long (at anthesis).

Extending from northern Borneo, throughout the Philippines to the northern Moluccas. Type: Lamao Forest Reserve, Luzon, *Meyer 2780.*

Primary and second-growth forest, from lowlands to 1000 m.

This species replaces the more westerly *A. diversifolium* which it closely resembles. It is characteristically larger in all its parts, particularly in the size of the individual flowers and the length of their pedicels. There are fewer flowers in an umbellule. The distinction between these two species is not always easy to make, especially when the material is fragmentary. A few specimens from the Philippines e.g. *Clemens 585, Merrill 1232* appear very similar to *A. diversifolium,* and it is possible that this species extends beyond Borneo. However, at present these specimens are regarded as part of the range of variation of *A. ahernianum*. Similarly, at least one specimen from southern Borneo (*Buwalda 7973*) approaches *A. ahernianum* in appearance.

5. **Arthophyllum engganoense** Philipson, *sp. nov.*

Arbor foliis imparipinnatis. Inflorescentia ramis in proprium officium mutatis et in coronam terminalem dispositis, quater ramificantibus; umbellulae pedicellis circa 5–10, c. 10–15 mm longis sub anthesi.

A tree to 21 m high, becoming glabrous. Lower leaves imparipinnate, multijugate, 60 cm long or more, petiole 24 cm long, 6 mm wide, petiolules 10–18 mm long; leaflets broadly elliptic to elliptic-oblong, c. 12–15 × 6–7 cm, base rounded with a short asymmetrical cuneate centre, apex shortly apiculate, margin entire often undulate chartaceous. Flowering branches c. 40 cm long; leaves opposite, simple or unifoliolate, ending in a whorl of simple leaves surrounding a compound umbel to 30 cm diam.; secondary rays about 8, c. 10–15 cm long, tertiary rays c. 8, slender c. 20–40 mm long, without bracts; pedicels c. 5–10 per umbellule, c. 10–15 mm at anthesis.

South Sumatra, Enggano Isd. Type: *Lütjeharms 4260* (Bogor).

Occurs in forest at low altitudes (up to about 100 m).

The two known collections of this species are very similar and contrast with the widespread *A. diversifolium* because of the few flowered umbelles with long, spreading pedicels.

6. **Arthrophyllum collinum** Philipson, *sp. nov.*

Arbor parva in prima aetate tomento rufo. Folia imparipinnate, foliolis oblongis, late ellipticis vel rotundis. Inflorescentia ramis in proporium officium mutatis et in coronam termnalem dispositis, quarter ramificantibus; bracteis rotundis, coriaceis.

Sparingly branched shrub or small tree up to 12 m high, all young parts with dense rufous tomentum. Leaves of the vegetative stems spirally arranged, imparipinnate, multijugate, up to 60 (or more) × 32 cm; leaflets oblong, broadly elliptic or rotund, up to 16 × 7 cm, coriaceous, margin entire slightly revolute, base truncate to rounded, unequal, apex rounded, obtuse, or shortly and bluntly apiculate, mid-rib prominent, lateral veins usually clearly visible below, upper surface frequenty rugose. Leaves of the flowering branches smaller with fewer pinnae or more frequently unifoliolate, leaflets more rotund and with longer petioles. Inflorescence a cluster of specialized leafy branches forming a terminal crown; the main rays up to 60 cm long, bearing one or more rarely two opposite pairs of usually unifoliolate rotund leaves.

Endemic to Borneo. Type: Sabah, Kinabalu, *Clemens 33195* (BM).

In forest and scrub from 600–2700 m, sometimes growing as an epiphyte in the crowns of trees.

The bark is grey and smooth, the wood pale and soft, and the cut stems exude a yellowish or orange latex. This species is characterized by the rotund coriaceous leaves on the flowering branches.

7. **Arthrophyllum crassum** Philipson, *sp. nov.*

Arbor parva in prima aetate tomento rufo. Folia imparipinnata, foliolis ellipticis oblongis vel lanceolatis. Inflorescentia ramis in proprium officium mutatis et in coronam termnialem dispositis, quater ramificantibus; bractea ovata plerumque acuta, rigidior alutaequa naturam habens, margine valde revoluta, nervis lateralibus obscurissimis.

Sparingly branched shrub or small tree up to 8 m high, all young parts with dense rufous tomentum. Leaves of the vegetative stems spirally arranged, imparipinnate, multijugate, up to 100 (or more) × 50 cm, of the flowering branches smaller with fewer pinnae or more frequently unifoliolate; leaflets elliptic, oblong or lanceolate, up to 24 × 7.5 cm, coriaceous, margin entire, strongly revolute, base cuneate to rounded, often oblique, apex narrowed to an acute often caudate apiculum, mid-rib prominent, lateral veins faint to obscure. Inflorescence a cluster of specialized leafy branches forming a terminal crown; the main rays up to 70 cm long, bearing an opposite pair (or rarely more pairs) of unifoliolate or (less frequently) pinnate leaves.

Endemic to Borneo. Type: Sarawak, Bako National Park, *Chai S18020* (Leiden).

Swampy peat forest and heath woodland, both primary and disturbed, from sea level to about 150 m. Some fragmentary collections (*Banying ak Nyudong S19404; Brunig S8720; Hewitt 770*) from higher altitudes (1000 m) further inland may belong to this species.

The leaves associated with the inflorescence are distinctively fleshy, have a strongly revolute margin and a smooth lower surface with indistinct lateral veins, and are ovate with rather acute apex. The leaflets of the pinnate leaves on the vegetative shoots are also rather leathery with indistinct lateral venation. The shrubs are occasionally epiphytic.

8. **Arthrophyllum pacificum** Philipson, *sp. nov.*

Arbor gracillis glabra, foliis imparipinnatis; foliolis plerumque ellipticis, c. 8–10 × 4–5 cm, membranaceis Inflorescentia ramis in proprium officium mutatis et in coronam terminalem dispositis, quater ramificantibus.

A slender tree to 14 m high, glabrous. Leaves of the vegetative stems spirally arranged, pinnate, multijugate, about 60 × 24 cm; of the flower-bearing branches smaller with fewer pinnae or simple; blade elliptic, oblong or avate, about 8–10 × 4–5 cm, rather membranaceous, mafgin entire, very slightly revolute, base abruptly cuneate, often oblique, apex obtuse, acute, or slightly apiculate. Inflorescence a whorl of specialized leafy branches forming a terminal crown to the vegetative shoots; the main rays 35 cm long bearing small pinnate leaves in opposite pairs.

Extending from the Moluccas to the Bismarck Archipelago. Type: Bismarck Archipelago, New Britain, Pomio subdistrict, *Isles et al NGF 34424* (Lae).

Primary forest on slopes of mountains, attaining Nothofagus mossy forest, from 800–2000 m. Reported as common in most localities.

All specimens from islands to the north of New Guinea are similar, in having more delicate foliage than *O. macranthum* from the mainland of New Guinea.

9. **Arthrophyllum diversifolium** Bl. Bijdr. Fl. Ned. Ind. (1826) 879. — *A. javanicum* Bl. l.c. — *A. ellipticum* Bl. l.c. — *Mormoraphis sumatrana* Jack. ex Wall. Cat n. 4931 (1831). — *Arthrophyllum blumeanum* Zoll and Moritz, Syst. Verz. Pl. Zoll. (1845-6) 41. — *A. ovalifolium* Jungh. and de Vriese in Ned. Kruid. Arch. 1 (1846) 19. — *A. ovatifolium* Jungh. and de Vriese in Ann. Sci. Nat. 3, 6 (1846) 117. — *A. dilatatum* Miq. Fl. Ind. Bat. 1 (1856) 768. — *A. diversifolium* var. *lanceolata* Miq. Fl. Ind. Bat. Suppl. 1 (1860) 340. — *A. blumeanum* var. *oblongatum* Miq. in Ann. Mus. Bot. Lugd. -Bat. 1 (1863) 27; var. *ellipticum* Miq. l.c.; var. *ovalifolium* Miq. l.c. — *A. borneense* Baker in Kew Bull. (1896) 23. — *A. congestum* Ridley in Journ. Fed. Mal. St. Mus. 10 (1920) 137. — *A. havilandii* Ridley in Kew Bull. (1933) 494. *A. rufo-sepalum* Ridley l.c. (1946) 40. — *A. rubiginosum* Ridley l.c. 41.

A small tree up to 14 m high, young parts with rufous tomentum. Leaves clustered at the end of the branches, spirally arranged on the vegetative shoots, imparipinnate or bipinnate (rarely tripinnate), multijugate, 150 cm long and 45 cm wide (wider in bipinnate leaves); usually in opposite pairs on the inflorescence-bearing branches and smaller with fewer pinnae or unifoliolate; leaflets ovate-oblong or elliptic, up to 24 × 11 cm ± coriaceous or membranaceous, margin entire, slightly revolute, base truncate, rounded, or cuneate, often oblique, apex shortly acuminate. Inflorescence a cluster of specialized leafy branches forming a terminal crown which abscises after fruiting; the main rays up to 150 cm long, bearing pinnate (or more rarely unifoliolate) leaves mostly in opposite pairs; the secondary rays up to c. 30 cm long, bearing mainly simple leaves in opposite pairs; tertiary rays (peduncles) about 5 cm long, articulate about the middle; pedicels ± 20, c. 5–12 mm long.

From the Malay Peninsula and Sumatra to Java, Borneo and Celebes. Type: Java, Salak, *Blume* (Bogor).

From sea-level to 1600 m, in a wide variety of habitats, from dry sandy soil to swampy humus. Occours in primary lowland and montane rain-forest and also in secondary forest, heath-forest and waste land.

The very widespread *A. diversifolium* is variable in many characters, and many comprise a number of geographic subspecies, but no basis for this is apparent at present. Most individuals have the lower leaves simply imparipinnate, whereas others have bipinnate, or rarely tripinnate, leaves. The flowers and inflorescences of these forms appear to be identical, though raipd changes in the umbellules after flowering produce a deceptively distinctive appearance in specimens at different stages of development. Field experience over the whole range of the species will be required to understand this interesting leaf-polymorphism. In treating all forms as one species I am partly influenced by the fact that most authors who have been familiar with the plants in Java (where both forms occur) have regarded the complex as a single species (the fact that some authors have recognized the variant from Salak as a distinct species does not affect the problem of leaf polymorphism).

Apart from the strikingly different leaf forms just discussed, certain local variants may eventually be shown to justify specific rank. A form growing on Salak (near Bogor) has often been regarded as distinct (see, for example, Hochreutiner in *Candollea* 2 (1925) 481, and Backer and Bakhuizen v.d .Brink, *Fl. Java* 2 (1965) 169). Indeed this form is the basis of the name *A. diversifolium*. I retain this name in preference to the other two names published simultaneously by Blume because it has been most consistently adopted since it was first used in this comprehensive sense by Clarke. On the evidence available I do not consider the Salak plants any more distinctive than many other local variants. It might be considered that *A. engganoense* is also no more than another such variant, but its facies is so marked that specific rank appears justified. It is possible that Ridley was correct in distinguishing *A. congestum*, but the material is not good and appears inadequate to confirm specific status. Five collections from Brunei and a neighbouring district of Sarawak are all very alike and sufficiently distinct from both *A. diversifolium* and *A. crassum* to suggest that they represent a further species: these are *Ashton S7840, Chew Wee-lek 981; Fuchs and Diederix 21182*; and *van Neil 3895 and 4312*. For the present these five gatherings are tentatively retained as a form of *A. diversifolium*. Similarly, the two collections described by Ridley as *A. rubiginosum* and *A. rufo-sepalum* are based on collections which are not altogether typical of *A. diversifolium*, but which come closest to that species. In the absence of more supporting material, it is advisable not to retain them as species. The first of these names (*A. rubiginosum*) has been widely used in identifications of Bornean specimens, but the specimens concerned are either typical *A. diversifolium* or belong to the distinctive *A. crassum.* Specimens from Mt. Kinabalu described by Ridley as *A. havilandii* have bipinnate leaves, and appear to conform well with *A. diversifolium.* This form was again collected on Mt. Kinabalu by Clemens and is also known from Sarawak (e.g. *Morshidi S24074*).

10. **Arthophyllum macranthum** Philipson, Bull. Brit. Mus. Nat. Hist. Bot. 1 (1951) 18.

Tree up to 25 m high, sparsely branched with leaves crowded at the ends of the branches, all young parts with dense rufous tomentum. Leaves of the vegetative stems spirally arranged, imparipinnate, multijugate, up to 100 × 30 cm; of the flower-bearing branches smaller with fewer pinnae, or simple; petioles; leaflets ovate to oblong, up to 16 × 8 cm, coriaceous, margin entire, revolute, base rounded, truncate, or cordate, very rarely cuneate, often oblique, apex obtuse or bluntly apiculate. Inflorescence a whorl of specialized leafy branches forming a terminal crown; the main rays up to 60 cm long, bearing pinnate leaves often in opposite pairs; the secondary rays about 10–20 cm long, bearing simple leaves, usually in opposite pairs, and terminating in umbellules or compound umbellules; umbellules with about 10–15 flowers; pedicels stout 3–5 mm long to 10 mm or more in fruit.

Endemic to New Guinea. Type: Morobe Distr. Boana, *Clemens 8433* (A).

Usually a sub-canopy tree of rain forest ranging from the lower montane zone to mossy subalpine woodland and scrubland. Occasional in second growth. Usually above 1000 m (up to 2700 m) but occurs on the coastal scarps of the Astrolabe range.

Trees become very different in appearance when in flower or fruiting: the spiral pinnate foliage leaves are surmounted by tufts of branches which end in inflorescences and bear much smaller leaves. The foliage leaves are fleshy, leathery and glossy. The ripe fruit is purple and shining. The bark is grey, at first smooth with many leaf-scars and lenticels, but small longitudinal fissures develop. The cut branches exude a brown latex and a scent of celery. The soft wood is white or straw coloured.

11. **Arthrophyllum papyraceum** Philipson, *sp. nov.*

Frutex in prima aetate tomento rufo, mox glabrescens. Folia imparipinnata, foliolis circa 7; foliola tenuia, plana, c. 12–24 × 5–10 cm. Inflorescentia umbella terminalis composita radiis primariis paucis.

A shrub rufous tomentose on the young parts. Leaves alternate, imparipinnate; leaflets about 7, membranaceous elliptic c. 12–24 × 5–10 cm, base broadly cuneate, apex finely acuminate, margin entire, slightly revolute. Inflorescence a terminal compound umbel; primary rays few (2), 2–3 cm long 2 mm wide, without bracts (caducous), secondary rays few (3) c. 13–18 mm long, articulated about the middle, ending in an umbellule of c. 10–12 flowers; pedicels 2–3 mm long slightly furfuraceous.

Sumatra, Type: East Coast: Loendoet Concession, Koealoe, near Aek Sordang. *Bartlett 6968* (Michigan).

Collected in primary rain forest.

Known from a single collection (with no duplicates) this species resembles *A. maingayi* in its simple inflorescence, and the few pinnae of its foliage leaves. However, the large size of the leaflets precludes its inclusion in that species.

12. **Arthrophyllum maingayi** Philipson, *nom. nov.* — "*A. pinnatum* (Lam.) Clarke" in Hook. f. Fl. Brit. Ind. 2 (1879) 734, excluding synonyms.

A low shrub or slender tree, rarely as high as 10 n, rufous tomentose on the very young parts, soon becoming glabrous. Leaves tufted at the end of the branches, spirally arranged, imparipinnate, usually with 5–7 leaflets (but up to 15), up to 30 × 18 cm; leaflets elliptic or elliptic-lanceolate, ± 8 × 3.5 cm, rather thin, base cuneate or rounded, apex apiculate or caudate, margin entire, slightly revolute, lateral veins faint and obscure. Inflorescence consisting of a number of primary branches radiating from the end of a leafy shoot; the primary branches, often rather few, usually 3–6 cm long and devoid of leaves except for a few terminal simple or 3-foliolate leaves around the compound umbels, occasionally the branches bear pairs of opposite leaves when they may be up to 30 cm long; secondary rays c. 2–3 cm long; pedicels 4–10 cm long.

Extending from Sumatra throughout the Malay Peninsula to Borneo. Type: *Maingay 679* (SING).

The name used by Clarke in Flora of British India has been in general use for this species. However, this name was based on *Pannax pinnatum* Lam. This in turn was based on the Rumphius name "*Scutellaria secunda*", which is quite a plant (*Polyscias pinnata*). Clarke therefore misapplied the name when using it for a Malay Peninsula *Arthrophyllum*, and a new name is necessary.

The three species *A. maingayi*, *A. montanum* and *A. alternifolium* are similar in having simpler inflorescences than *A. diversifolium*. *A. montanum* can be distinguished from *A. maingayi* by its more leathery leaves with more prominent nervation, and by the more woody and leafy flower-bearing primary branches of the inflorescence. *A. alternifolium* is distinguished from both these species by its small coriaceous leaflets with inconspicuous nervation. Most specimens can be readily distinguished, but a few can be asigned to a species only doubtfully, usually because the material is inadequate. This is usually due to the junction between the vegetative (spiral phyllotaxtic) shoots and the flower-bearing branches being omitted.

13. **Arthrophyllum kjelbergii** Philipson, *sp. nov.*

Arbor parva in prima aetate tomento rufo. Folia imparipinnata, foliolis ellipticis vel ovate-oblongis, ad 8 × 3.3 cm, chartaceis. Inflorescentia ramis in proprium officium mutatis et in coronam terminalem dispositis, ter ramificantibus.

A small tree, 10 m high, branches c. 1 cm diam., the young parts covered in rufous tomentum. Leaves clustered towards the ends of the branches, spirally arranged on the vegetative shoots, imparipinnate, multijugate, 25–30 × 16 cm; leaflets elliptic or ovate-oblong, up to 8 × 3.3 cm, chartaceous, margin entire minutely revolute, base rounded to cuneate often oblique, apex tapered to a blunt apiculum, or rounded and mucronate. Inflorescence a terminal cluster of c. 5–10 specialized branches; primary rays c. 15–20 cm long, 1.5–2.0 mm wide bearing near the middle an opposite pair of simple leaves or sometimes trifoliate leaves, and 2–3 similar leaves below the terminal cluster of secondary rays; secondary rays c. 12, c. 2.5 – 3.5 cm long, terminating in an umbellule of about 12 flowers.

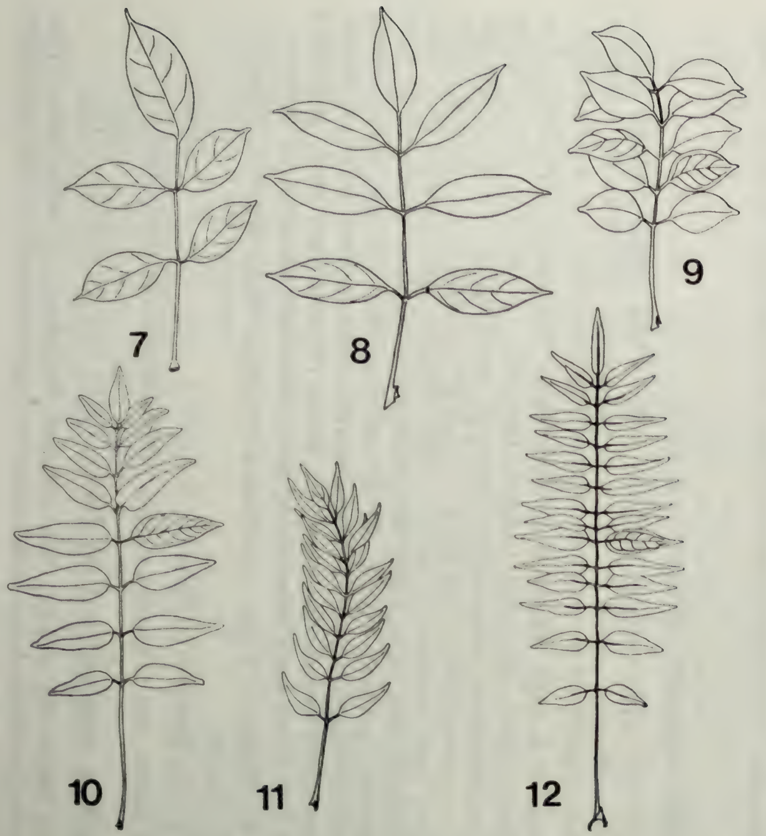
Endemic to Celebes. Type: South-east Celebes: near Kendari, Sangona, *Kjellberg 1145* (Bogor).

In primary rain forest 50–150 m.

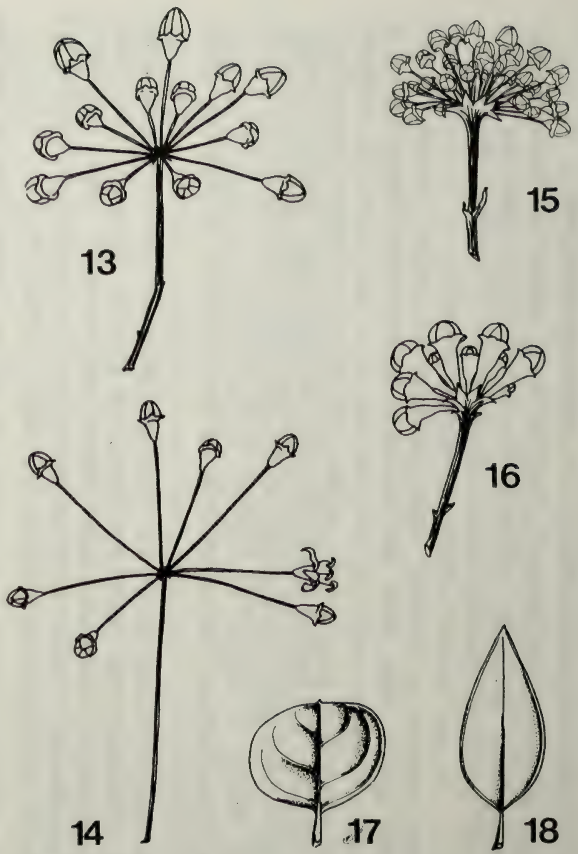
The small leaves and relatively simple inflorescences are distinctive.

14. **Arthrophyllum cenabrei** Merr. in Philip. Journ. Sci. 20 (1922) 417.

A glabrous tree c. 10 m high, the ultimate branches c. 5 mm diam. Upper leaves pinnate, up to 10 cm long, leaflets mostly 5, sometimes 3, or the uppermost



Figs. 7–12. Foliage leaves (all × 1/5). 7, *A. maingayi;* 8, *A. montanum;* 9, *A. pulgarense;* 10, *A. kjellbergi;* 11, *A. alternifolium;* 12, *A. ashtoni.*



Figs. 13–16. Umbellules (all × 1). 13, *A. ahernianum;* 14, *A. engganoense;* 15, *A. diversifolium;* 16, *A. macrantum.*

Figs. 17–18. Bracts (× ⅓). 17, *A. collenium,* 18, *A. crassum.*

reduced to simple leaflets, the rhachis and petiole c. 4 cm long, the leaflets mostly elliptic, 4.5–6 × 2.5–3.5 cm, chartaceous to subcoriaceous, very shortly and obtusely acuminate, base acute, brownish olivaceous and slightly shining when dry. Peduncels c. 4 cm long, umbellately arranged at the tops of the branchlets, usually however with solidary inflorescences in the axils of the uppermost leaves, thus forming a somewhat leafy inflorescence.

Endemic to the Philippines. Type: Cebu, *Cenabre and de la Cruz FB28343* (n.v.).

On slopes at 600 m.

No specimen of this species has been located. The above description is taken from Merrill's original account. In placing this species in the key, it has been assumed that the inflorescence branching is relatively simple.

15. **Arthrophyllum pulgarense** Elmer in Leaflets Philipp. Bot. 7 (1915) 2551.

A small tree, branches c. 1 cm diam., young parts with red tomentum, becoming glabrous except on the ovaries. Leaves clustered towards the ends of the branches, spirally arranged on the vegetative branches, imparipinnate, about 6 pairs of leaflets, c. 22 × 8 cm; leaflets elliptic to rotund, c. 4 × 2.8, coriaceous, margin entire, revolute, rounded to broadly cuneate, apex rounded or abruptly tapered to a short obtuse apiculum. Inflorescence a terminal cluster of specialized branches; primary rays c. 6–10 cm long, 3–4 mm wide, bearing near the middle an opposite pair of simple rotund leaves, and with a whorl of similar leaves below the terminal cluster of secondary rays; secondary rays c. 6–8, 2–4 cm long terminating in an umbellule of about 8–12 flowers, bracts caducous.

Endemic to the Philippines. Type: Palawan, *Elmer 13193* (PNH).

Common in montane forests on Mt Pulgar.

The coriaceous small often rotund leaflets are characteristic.

16. **Arthrophyllum montanum** Ridley in Journ. Fed. Mal. St. Mus. 4 (1909) 24. — *A. nitidum* Ridley l.c. 7 (1916) 42. — *R. ovatum* Ridley l.c. 42.

Shrub or small tree to 6 m, unbranched or sparingly branched, rufous tomentose on the young parts, becoming glabrous. Leaves tufted at the ends of the branches, spirally arranged, imapripinnate, multijugate, about 30–55 × 12–22 cm; leaflets elliptic or oblong 6–10 × 2.5–4 cm, coriaceous or charactaceous, base cuneate, apex with a short blunt apiculum, margin entire, revolute, the few principal lateral veins usually rather prominent; the leaves associated with the umbels usually unifoliolate, broadly elliptic to rotund. Inflorescences on specialized leafy branches either in terminal clusters or axillary in the upper leaves; the branches 10–30 cm long, leaves mostly simple in opposite pairs, the branches ending in a whorl of simple leaves surrounding a compound umbel.

Malaya Peninsula. Type: Pahang, *Ridley 13687* (SING).

Primary forest ascending to montane zone, and in second growth, 250–1500 m.

Similar to *A. pinnatum* but distinguished by the more leathery leaves and by the leafy inflorescence branches which are usually absent in *A. pinnatum*.

17. **Arthrophyllum alternifolium** Ridley Fl. Mal. Pen (1922) 886. — *A. pinnatum* Clarke in Hook. f. Fl. Brit. Ind. 2 (1897) 734, pro parte; King in Journ. As. Soc. Bengal 67 (1898) 59, pro parte. — *A. alternifolium* Clarke l.c., in synon.

A slender sparingly branched shrub, to 2 m high, rufous tomentose on the young parts, becoming glabrous. Leaves tufted at the ends of the branches, spirally arranged, imparipinnate, multijugate, about 20–25 (30) × 9–12 (15) cm;

leaflets ovate, elliptic or lanceolate, 3.5–4 (6) × 0.9–2 (2.3) cm, coriaceous, base cuneate, apex acuminate to caudate, obtuse, margin entire, revolute, veins obscure; the leaves associated with the umbels (if any) reduced, with fewer leaflets or unifoliate, sometimes broadly ovate. Inflorescence usually a terminal compound umbel, occasionally a whorl of leafy branches (5–14 cm long) each ending in a compound umbel.

Malay Peninsula. Type: Malacca, *Griffith 2676* (SING).

In shady montane forest, with *Rhododendron* and *Dacrydium*, 3000 ft and above.

The small coriaceous, often apiculate, leaflets are characteristic. Although collected most frequently on Mt Ophir it occurs on other high ridges in the southern Peninsula.

INSUFFICIENTLY KNOWN SPECIES

A. reticulatum Bl. ex Miq. in Ann. Mus. Bot. Lugd. -Bot. 1 (1863) 27.

The original description was based on foliage leaves only. Their place of origin was uncertain. Since I have seen no specimen identified as this species, its identity cannot be decided.

A. serratifolium Miq. Fl. Ind. Bat. Suppl. (1860) 341.

The original description was based on foliage leaves only. I have seen no specimen identified as this species, but since all other members of the genus have entire margins to the leaflets, I doubt if this species would prove to be a true *Arthrophyllum*.

I wish to thank Dr E. Edgar of Botany Division, D.S.I.R., Christchurch for writing the Latin diagnoses.

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